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The Larval Behavior, Life History Traits, and Adaptations to Predation and Competition of *Dendrobeania lichenoides* (Bryozoa, Cheilostomata).

by

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Abstract

THE LARVAL BEHAVIOR, LIFE HISTORY TRAITS AND INTRA-COLONIAL ADAPTATIONS TO PREDATION AND COMPETITION OF DENDROBEANIA LICHENOIDES (BRYOZOA, CHEILOSTOMATA)

Catherine Drew Harvell

Chairperson of supervisory committee: Dr. Fu-Shiang Chia

Dendrobeania lichenoides, an abundant, foliose bryozoan in the San Juan Archipelago fouling community, has larval and adult traits which contribute to its spatial competitive ability and reduce the extent of grazing by nudibranchs. The competitive superiority of Dendrobeania in substrate interactions with other colonial invertebrates is demonstrated by analysis of overgrowth interactions. Adult colonies are elevated above the substrate by attachment rhizoids which allows them to overtop encrusting organisms, supporting the hypothesis of Buss (1980) and Jackson (1979) that a vertical growth component is advantageous to successful overgrowth competitive interactions. The rhizoids, in addition to attachment, probably serve to elevate both the ancestrula and the colony above potential competitors for space.

Various adaptations to nudibranch grazing were observed in Dendrobeania lichenoides. Habitat selection behaviors of Dendrobeania larvae may serve to reduce predation on colonies by directing larvae to "refuge" habitats, e.g., on polychaete tubes (Eudistylia vancouveri) which appear inaccessible to large nudibranchs. When colonies are accessible to nudibranch grazers, they are characteristically grazed on the outer colony margins, leaving only the inner regions which are firmly attached to the substrate with rhizoids. Experiments suggest that reduced palatability, perhaps due to high numbers of brown bodies in the inner colony may also reduce the extent of nudibranch grazing damage.

Individual Dendrobeania lichenoides colonies and most other colonial invertebrates are only partially consumed by their predators, raising the question as to why predators should forage partially among several colonies, rather than consuming them in their entirety (Birkeland and Gregory, 1975). The interaction of Dendrobeania with its predators emphasizes the role of prey defenses in limiting the extent of grazing damage and in controlling the grazing pattern of predators. Although little evidence exists for the role of this phenomenon in structuring other invertebrate-grazer interactions, these results can be compared to those obtained for plant-herbivore interactions, where herbivore-induced plant defenses have been shown to limit and control herbivore population fluctuations (Haukioja, 1980).

Life history characteristics may vary with growth form in colonial invertebrates (Jackson, 1979). Dendrobeania lichenoides, which has a

plate-like growth form, is relatively long-lived (more than 1.5 years) has a late time of first reproduction (up to 4 months after settlement), a seemingly low fecundity, a flexible skeleton and special attachment rhizoids. The predictions which Jackson (1979) makes for colonial invertebrates with a plate-like growth form are supported by this study, suggesting that it is possible to predict life history characters from colony form.

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GENERAL INTRODUCTION

Recent studies have stressed the importance of competitive interactions for space in determining the success or fitness of individual bryozoan colonies (Buss, 1980; Jackson, 1977, 1979; Stebbing, 1973). Because bryozoans (and other colonial invertebrates) are largely sessile and often live in space-limited habitats, their competitive strategies must differ from those of motile invertebrates. Competition between bryozoans is often mediated through overgrowth interactions, in which the superior spatial competitor overgrows the inferior (Jackson, 1979). Little consideration has been given the role of predation in mediating competitive interactions or in the dynamics of individual colonies.

This study was designed to examine some of the adaptations of Dendrobeania lichenoides, a cheilostome bryozoan, to predation and competition and to test some general predictions about life history traits and colony form using this species as a model.

The interactions of colonial invertebrates with their predators are not well-studied; little is known about grazing on non-plant organisms (grazing is here considered synonymous with partial predation and means removing parts of a resource which can regenerate). Recent studies of fish grazing on scleractinian corals (Neudecker, 1979) and gastropods grazing on gorgonian corals (Birkeland and Gregory, 1975) have shown that a considerable quantity of living tissue can be consumed without causing prey mortality. Studies of nudibranch grazing on bryozoans have been mostly concerned with

the implications for nudibranch feeding biology and ecology (McBeth, 1971; Nybakken and McDonald, 1981; Seed, 1976) and have not detailed the ecological consequences of such partial predation to individual colonies or discussed variation in grazing preference for different regions of colonies.

The role of larval substrate selection behaviors and ancestrular orientation has received little attention in determining the outcome of competitive and predatory interactions involving bryozoans. Zimmer and Woollacott (1977) have reviewed the literature about bryozoan metamorphosis and initial colony development and Ryland (1976; 1977) has reviewed studies about bryozoan larval behavior and taxes and tropisms of bryozoan larvae and colonies. Jackson (1979) discussed the importance of orientation in determining the outcome of competitive interactions, but didn't discuss orientation of colonies early in astogeny. The study of Young and Chia (1981) showed that some bryozoan larvae (Bugula pacifica) can delay metamorphosis in the presence of a dominant competitor, and therefore provided one of the few studies detailing selective pressures governing bryozoan larval behaviors. Grosberg (1981) demonstrated that a whole suite of larvae including many colonial species avoided settling near a dominant competitor.

Life history characteristics may vary with growth form in colonial invertebrates (Jackson, 1979). Jackson (1979) used literature reports, observation and theoretical considerations to predict life history traits which should correspond with different definable, growth form types. More information is needed to test these pre-

dictions.

Dendrobeania lichenoides (Robertson, 1900) is a dominant component of the fouling community (organisms attached to man-made structures) and is patchily abundant on subtidal rock walls in the San Juan Archipelago, Washington, U.S.A. The genus Dendrobeania has been recorded from temperate and subarctic oceans of the world (d'Hondt, 1979; Gosner, 1971; Hayward and Ryland, 1977; Osburn, 1954; Silen, 1941), but the species range extends only from San Francisco, California into Alaska (Osburn ,1954; Robertson, 1900). Dendrobeania lichenoides (hereafter referred to as Dendrobeania) has not been previously studied.

The plate-like growth form of Dendrobeania is unique among bryozoans of the San Juan Archipelago. Each colony is composed of several broad, flexible fronds which project from a central zone of basal attachment and are attached to various substrata by rhizoids (rootlets). Each frond of the colony is composed of numerous skeletal boxes (zooecia) housing individual (but connected) feeding polyps which filter plankton from the water with a circular array of ciliated tantacles called a lophophore. Although colonies are often recumbent, at the height of summer growth they may become folded and contorted into an upright form (Fig. 1).

In this study, all observations on Dendrobeania are from nearshore waters in the San Juan Archipelago (Fig. 2). Experimental work and colony collections using SCUBA largely involved dense populations growing underneath the Friday Harbor Laboratory (FHL) breakwater and the Friday [redacted] Town docks. Subtidal observations

were also made on vertical, overhung, rock walls at Turn Island, Point George and Rosario; intertidal observations were made at Pile Point, San Juan Island and Bamfield Inlet, Bamfield, British Columbia (Fig. 2).

In chapter one, some of the factors governing colony habitat selection and orientation are described. These include larval photic and substrate selection behaviors as well as factors influencing ancestrular elevation. In Dendrobeania, unlike most bryozoans, the original substrate attachment formed at metamorphosis is subsequently replaced with a rhizoid (rootlet) which effects colony elevation and maybe colony orientation. By considering the interactions of Dendrobeania with some of its competitors and predators, the biotic selective pressures which could have played a role in the evolution of larval behaviors and ancestrular morphology is considered.

In chapter two, seasonal growth and fecundity data are used to examine certain general predictions made by Jackson (1979) about growth form and life history traits of colonial invertebrates, i.e. that life-history traits (relative growth rate, fecundity, colony longevity and age of first reproduction) should correspond predictably with growth from categories into which most colonial invertebrates fall.

In chapter three, some general characteristics of predation on colonial invertebrates are considered, based on observations of nudibranch grazing on Dendrobeania. Because the grazers (Triopha catalinae [Cooper], Arminacea; Dirona albolineata [Cockerell and Elliott] and D. aurantia [Hurst], Arminacea) only partially consume each colony they are termed "partial predators" (Jackson and

Palumbi, 1979). The consistent manner with which these nudibranch species graze Dendrobeania was documented, and intra-colonial variation in placement of reproductive and defensive structures was examined to determine if they corresponded with the observed nudibranch grazing pattern.

CHAPTER ONE

LARVAL BEHAVIOR AND ANCESTRULAR REATTACHMENT: ROLE OF THE SELECTIVE PRESSURES OF COMPETITION AND PREDATION

LARVAL BEHAVIOR AND ANCESTRULAR REATTACHMENT: ROLE OF THE SELECTIVE PRESSURES OF COMPETITION AND PREDATION

INTRODUCTION

For sessile, colonial, marine invertebrates the proximity of colonies to a superior competitor for space, their accessibility to predators or their settlement on an inappropriate substrate can result in mortality or reduced reproductive output (Buss, 1979; Jackson, 1979; Young and Chia, 1981). Also, the orientation of a colony relative to its substrate and to potential competitors can also be critical to fitness and survival (Buss, 1979; Jackson, 1979). Because of their permanent attachment to the substrate after metamorphosis, dispersal and habitat selection of sessile invertebrates can only occur during the larval pelagic or benthic crawling phases (Buss, 1979; Palmer and Strathmann, 1981). Buss (1979) predicted that larval habitat selection will occur in sessile, colonial, marine invertebrates when the location of a microhabitat that is predictably associated with high survivorship or reproductive output can be sensed by a recruiting larva. If, however, favorable microhabitats are not recognizable by the larva, post-metamorphic growth tropisms should be important in determining colony position.

Most larvae can locate favorable microhabitats by using a variety of physical and biotic cues, e.g., substrate rugosity (Crisp, 1976), light (Graves, 1930; Ryland, 1976; Thorson, 1964), temperature, salinity, and currents (Ryland, 1976), microhabitat fungal, faunal, and floral characteristics (Ryland, 1976; Strathmann et al, 1981), and the presence of conspecifics (Knight-Jones, 1951; Woodin, 1976) or potential prey (Bickell and Chia, 1979; Chia and Koss, 1978). Larvae can also

avoid habitats made unfavorable by the presence of a superior competitor (Grosberg, 1981; Young and Chia, 1981).

After settlement, the time at which orientation of the colony becomes established may vary considerably among bryozoans (Ryland, 1976) and other sessile invertebrates. Most bryozoans establish permanent attachment and therefore colony orientation at metamorphosis (Ryland, 1976; Zimmer and Woollacott, 1977), although growth tropisms can subsequently influence the direction and rate of growth (Buss, 1979; Schneider, 1974). Reorientation of bryozoan ancestrulae following initial attachment occurs in at least two different bryozoan orders (Bullivant, 1968; Silen, 1980). In both cases studied, reattachment was effected by downward growth of a rhizoid or stolon which lifted ancestrulae above the substrate and consequently forced loose the original substrate adhesion. The functional significance of this type of reorientation is not known, but its occurrence in divergent taxa suggests a more general phenomenon than previously believed.

The small-scale spatial distribution of colonial marine invertebrates may be controlled by one or more of three variables: larval habitat selection, differential mortality, or directional growth. Directional growth (Buss, 1979) is probably of less importance to determinately growing taxa which are constrained by their growth form; their distribution may be largely a function of larval habitat selection or differential mortality. Determinate is used here as in Jackson (1979) to refer to those taxa with a relatively fixed growth form and variable (through ontogeny) growth rate, e.g., taxa whose initially rapid growth slows as the colony reaches its final form. Indeterminate taxa, which have no fixed adult size (Sebens, 1977), grow at a constant rate through the colony life

and possess no fixed growth form; they can readily grow in any direction (Buss, 1979). The morphology of indeterminately growing taxa may be largely determined by food supply, habitat, and biotic interactions rather than by a pre-determined genetic pattern (Jackson, 1979; Buss, 1979). Encrusting colonies with indeterminate growth may alter their form to encircle or grow away from a biotic or physical obstruction (Ryland, 1977; Buss, 1979; Jackson, 1979).

In this study, Dendrobeania lichenoides, a determinately growing bryozoan in the fouling community, was most frequently found attached to polychaete tubes and less frequently to various species of tunicate and the dock undersurface. Larval photic and substrate selection behaviors were examined to explain observed colony distributions. Because larval behavior may evolve as a response to some discernible selection pressure (Doyle, 1974), the attempt was made to locate selective agents favoring observed behaviors.

The importance of colony orientation to biological (Jackson, 1979) and physical (Ryland, 1976) factors has been discussed, but pre-metamorphic orientation to water currents is the only demonstration of its occurrence (Ryland, 1976). Post-metamorphic ancestular reattachment (and perhaps reorientation) was observed in Dendrobeania; the morphological mechanism and selective pressures favoring it are also considered in this chapter.

MATERIALS AND METHODS

All animals were collected underneath the floats at Friday Harbor Laboratories (F.H.L.), Washington, U.S.A. and under the Friday

Harbor Town Docks where Dendrobeania colonies were commonly found attached to Eudistylia vancouveri tubes (Polychaeta), the tunics of Boltenia villosa, Styela gibbsii, and Chelyosoma productum (Ascidia) and the styrofoam or plastic float undersurface.

Larval hatching was induced in the laboratory by exposing mature colonies in flowing sea water to light after an 8 hour dark period. Free-swimming larvae were then pipetted into culture dishes for observation and experimentation.

Substratum preferences of Dendrobeania larvae were tested in the laboratory. Four 1 cm^2 substrates were offered in each bowl: 1) Boltenia villosa tunic, 2) Styela gibbsii tunic, 3) the growing, young margin of Eudistylia vancouveri tubes, and 4) an older portion of the E. vancouveri tube. Fifty larvae were pipetted into each of 10 500 ml culture bowls, which were placed under dark covers in the sea table. The numbers of larvae settled on each substrate were censused 24 hours later. After determining that the variances in numbers of larvae settled on each substrate were homoscedastic with an F-max test (Sokal and Rohlf, 1969), an Analysis of Variance (ANOVA) was used to determine if there was a significant difference among any of the treatment means (Sokal and Rohlf, 1969; Michigan Interactive Data Analysis System [MIDAS], Fox and Guire, 1976). Pairwise comparisons of means were made with a Scheffés test (Fox and Guire, 1976).

Larval phototropic behavior was examined at night in December, 1979, by pipetting 25 larvae immediately upon their release from colonies into a glass tube 30 cm long and 1 cm in diameter. The

tube containing filtered sea water was sealed after the introduction of larvae, then immersed horizontally into a seawater table at ambient (9 - 10°C) sea temperature. All room lights were extinguished except an 80 foot candle light illuminating from one end of the tube. The tube was marked into three 10 cm segments and the number of larvae in each of the three segments was recorded approximately every 10 minutes for two hours. Light levels were measured with a Li-Cor Py516-7601 photometer.

To test for a shade preference at settlement, swimming larvae were placed in petri dishes with covers. One half of each dish was masked top, sides, and bottom with black electrical tape, creating a dish with a shaded and unshaded half. Tests were usually initiated at least 8 hours before darkness and usually in the morning. After 24 hours, the number of larvae in the shaded and unshaded halves was recorded (technique after Young and Braithewaite, 1980).

The competitive status of Dendrobeania was determined by analyzing interspecific contacts with other colonial animals on 11 20 x 20 cm linoleum plates, which were submerged for one year in July, 1980. (The plates belonged to Chuck Greene who allowed me to take information about Dendrobeania interactions from them.) The contact was scored as an overgrowth for Dendrobeania if it grew on top of and covered a subordinate. This method has been used by a number of researchers to examine interference competition in space-limited systems (Jackson, 1979; Jackson and Buss, 1975; Quinn, 1979; Stebbing, 1973). No attempt was made to determine if the subordinate was injured by the interaction. The null hypothesis that Dendrobeania is an equal or

poorer competitor than all other taxa on the plates was tested with a Student's t-test (Sokal and Rohlf, 1969).

Size-frequency data for Dendrobeania colonies were collected in the field, underneath the Friday Harbor Town docks using SCUBA. Two areas ($4m^2$ blocks) were randomly selected from the surface prior to the dive. The greatest diameter of each colony in each block was measured and placed into one of three size classes: 0 - 2.0 cm, 2.0 - 4.0 cm, and 4.1 or greater. Measurements included colonies attached to the dock surface, to ascidians and to polychaete tubes.

RESULTS

Larval Phototropisms

When released into a tube illuminated from one end, newly hatched swimming larvae initially congregated at the lighted end (Fig. 3). Numbers of larvae in the lighted end (80 foot candles) declined after about an hour; simultaneously, numbers of larvae at the darker end (10 foot candles) increased (Fig. 3). There were fewer larvae at the end of the experiment because some began settling on the walls after becoming photonegative. For this reason, only swimming larvae were counted.

Larval Substrate Selection

In the field, Dendrobeania colonies were commonly found attached to primary substrata such as rock, cement, styrofoam, rubber tires, and as epibionts on the tunicates Chelyosoma productum, Pyrua haustor, Styela gibbsii, and Boltenia villosa; the polychaete tubes of Schizobranchia

insignis and Eudistylia vancouveri, the algal holdfasts of Laminaria saccharina, Hedophyllum sessile, and Phyllospadix sp.; the armored sea cucumber Psolus chitonoides and the epizoanthid anemone, Epizoanthus scotinus.

Laboratory substrate tests indicated that larvae settled in greater numbers on E. vancouveri tubes than on other substrates offered (Table 1). They settled in considerably greater numbers on older portions of worm tubes than on all other substrates offered and discriminated between squares cut from old portions of the tube and the younger portions which were located nearer the feeding tentacles of the worm. Larvae settled in statistically indistinguishable numbers on young tube portions and on Styela gibbsii tunics, although in slightly higher numbers on worm tubes. Settlement on Boltenia villosa tunic was the lowest and was statistically different from all other treatments at $p < 0.004$.

In the laboratory, larvae consistently settled in shaded areas of petri dishes. In experimental dishes, 80% of the larvae (n= 261) settled on the sides or bottom of the shaded halves of dishes (Fig. 4).

Ancestrular Reattchment

The post-larva (pre-ancestrula) is initially (one to two days) a rounded encrustation on the substrate which subsequently elongates (Fig. 5a). At four days, a rhizoid grows down from the ventral surface of the pre-ancestrula, contacts the substrate, and by continuing to grow, frequently detaches the ancestrula from its original connection to the substratum and lifts it up (Fig 5b). The ancestrula may be

Table 1. Analysis of variance testing for differences among numbers of larvae (n= 50/trial) settled on four different substrates offered, 9 trials.

Source of variation	SS	MS	F
Among substrates	428.07	142.69	10.89***
Within substrates	471.90	13.10	

Scheffes difference between means

Boltenia	Styela	Eudistylia tube (young)	Eudistylia tube (old)
(1.5)[1]	(6.5)	(7.5)	(10.6)

$p^2 < 0.54$ $p < 0.06$

$p < 0.02$

1 mean number of larvae/cm^2 replicate (n= 9 replicates)
2 all probabilities between means are 0.007 or less unless otherwise noted
*** probability level of $p < 0.001$

lifted up to 0.5 mm above the substrate by 6 days post-settlement.

Competitive Ranking

Dendrobeania was the dominant competitor as measured by overgrowth interactions on panels submerged for 1 year (Table 2). It significantly overgrew the two most abundant taxa on the panels, the bryozoans Tegella aquilirostris and Cheilopora praelonga ($p < 0.01$ and 0.001, respectively). In most of the 24 cases where T. aquilirostris overgrew portions of Dendrobeania, the "attack" was initiated from the proximal, more attached regions of the colony rather than at Dendrobeania's upraised growing distal margin. The bryozoan Schizoporella sp. and the sponge Haliclona permollis were not involved in enough interactions to yield a significant result.

Predation

Fifty-eight percent (n= 571) of colonies surveyed on 3 F.H.L. dock transects in October showed clear evidence of nudibranch grazing. Field observations suggest that E. vancouveri tubes may be a refuge from predation by some large nudibranchs such as Triopha catalinae Dirona albolineata, and D. aurantia. This hypothesis was tested by comparing sizes of colonies on primary substrata (dock), which were readily available to nudibranchs, with sizes of those colonies on polychaete tubes and tunicates which may have been less accessible. A greater proportion of large colonies were attached to worm tubes and tunicates than to the dock (Table 3). In addition, more colonies

Table 2. Outcome of pairwise overgrowth interactions between *Dendrobeania* and other colonial taxa on linoleum plates (20 x 20 cm) submerged for one year.

Taxon	Number of wins	Number of losses	Significance of win for *Dendrobeania* df	p
Tegella aquilirostris	24	54	150	0.01
Cheilopora praelonga	3	37	78	0.001
Schizoporella sp.	2	5	12	ns
Haliclona permollis	0	1		ns
Total	29	77	210	0.001

df degrees of freedom
p probability level

Table 3. Percentage of Dendrobeania colonies in each of three size classes found attached to different substrates.

Substrate	Size Class			
	0-2.0 cm	2.1-4.0 cm	greater than 4.0 cm	# colonies in 2 $2m^2$ quadrats (n)
Polychaete tube	55% (73)*	43% (45)	11% (14)	132
Tunicate tunic	65% (22)	26% (9)	10% (2)	33
Dock	61% (14)	39% (9)	0	23

* numbers in parentheses are actual frequencies

in a given area were located on polychaete tubes than on tunicates or the dock. Ten nudibranchs (including at least one of each species) were released in the area surveyed for size distributions; two weeks later none of the colonies attached to the worm tubes appeared disturbed, although colonies attached to the dock and some attached to tunicates were severely grazed. Large nudibranchs were never seen crawling on worm tubes throughout the study, although Dendrobeania was abundant on them.

DISCUSSION

Larval behaviors strongly influence the field distribution of Dendrobeania colonies. A whole suite of such behaviors interact to determine where larvae settle, including: 1) short initial photopositivity allowing brief dispersal, 2) subsequent photonegativity and shade preference at settlement promoting retention under the docks, and 3) specific substrate preferences initiating the association with refuge habitats.

Initial photopositivity, subsequent photonegativity and shade settlement is common for taxa living on undersurfaces in shallow water, such as intertidally (Thorson, 1964). Attraction to light keeps larvae in surface waters, which will eventually carry them to the intertidal; shade seeking leads larvae under rocks and other structures where they will eventually settle. Another common larval photic response is constant photopositivity until settlement, which occurs in taxa settling on upper, lighted shallow water surfaces (Ryland, 1976; Thorson, 1964).

Larvae may also discriminate between types of substrates. Consistent discrimination between old and young portions of the same worm tube provides a mechanism explaining the observed field distribution of Dendrobeania colonies on older tube portions of worm tubes and allows rejection of the differential mortality hypothesis. Settlement on older tube portions away from the filtering polychaete tentacles prevents consumption of settling Dendrobeania larvae by the polychaete and competition between the young colonies and the polychaete for food. Larvae may age worm tube sections by age-related intra-tube gradients in micro-faunal and floral density or composition. Older tube portions were noticably more fouled with epibionts than younger portions. Although there may be other adaptive reasons for larval settlement on older tube portions as discussed below, it is also possible that larvae settle there only because of the richer epibiotic growth.

To test the hypothesis that colony fitness is higher on polychaete tubes, the preferred substrate, diameters of colonies on a variety of substrata were measured. Colonies on polychaete tubes and tunicates had slightly greater diameters than those attached directly to the dock. Although there may be other, unknown causes such as increased access to feeding currents on worm tubes and tunicates, greater diameter may also result from lower nudibranch grazing pressure on epibiotic colonies. If so, then there is strong selection to settle on other organisms if the associated costs (e.g., competition with the host for food) are not high. Worm tubes may be an unstable substrate which nudibranchs avoid and tunicates may act as a surface obstruction hinder-

ing foraging efficiency. In addition, because the worm tubes are 0.5 to 1 meter long and extend that far into the water column, a large nudibranch crawling on the tube would be highly visible to potential fish predators. Large nudibranchs are toxic or distasteful to most fish tested (Paine, 1965) but small nudibranchs are heavily preyed upon by fish (Harris, unpublished data) and "uneducated" fish may prey upon large ones.

After larvae have located a suitable substrate they undergo metamorphosis (the rapid morphogenetic transition to a sessile adult colony), at which time most bryozoans become permanently attached to the substrate via the metasomal sac (Silen, 1980; Zimmer and Woollacott, 1977). As mentioned, in the Dendrobeania the initial attachment with the metasomal sac is frequently replaced at 4 - 5 days after settlement with a rhizoid which grows down and elevates the ancestrula above the substrate. While the process may differ among bryozoan groups, secondary attachment and subsequent elevation of ancestrulae by rhizoids or stolons occurs in some anascan cheilostomes (Silen, 1980), ascophoran cheilostomes (Harmelin, 1977), and cteno-stomes (Bullivant, 1968). As discussed below, three non-mutually exclusive functions for ancestrular elevation by a stalk are: 1) elevation above the substrate where competition and perhaps predation are more intense, 2) elevation above the substrate where sediment may accumulate, and 3) provision of a less rigid substrate attachment.

Growing area in the space-limited fouling community may be an important resource for Dendrobeania ancestrulae; consequently, slight

elevation above the substrate (where other competitors abound) may be advantageous. Elevated 4 - 8 zooid colonies on fouling plates were occasionally observed growing above other bryozoan ancestrulae. Mature Dendrobeania colonies overgrow most other sessile taxa encountered in competitive interactions, probably because their attachment rhizoids act like stilts, supporting the growing margin above the substrate and competitors. The competitive advantage of an upraised margin in bryozoan overgrowth interactions was suggested by Jackson (1979) and Buss (1980). In addition, reattachment may allow colonies to reorient to a competitor detected after settlement. Dendrobeania colonies initially grow proximally and distally at settlement (see Chapter 2 for discussion of astogeny), leaving the lateral margins of the ancestrular area only slightly upraised; this is the area overgrown by competing species. Reorientation could direct the upraised growing edges toward a competitor. Detection of and directional growth towards an upcurrent, subordinate competitor has been observed for a tropical milleporid hydro-coral, and is a method of reaching a predictable substratum (Wahle, 1980).

Predation by flatworms (Osman, 1981; pers. obs.) or small nudibranchs (1 cm or less) which attack anascan bryozoans through their frontal membrane (Yoshioka, 1973) may also provide a selective force for elevation. Access to the frontal membrane, which is located on the upper surface of the ancestrula may be more difficult for these micro-predators.

Finally, Silen (1980) suggested that ancestrular elevation by a rhizoid in an erect anascan bryozoan, Scrupocellaria reptans, provided

an elastic attachment and decreased the problem of sedimentation. An elastic substrate attachment may be important to colonies such as S. reptans which typically attach to flexible algae. Sedimentation has been suggested as a factor limiting bryozoan colonization and survival in some habitats (Schopf et al, 1980), therefore slight elevation above the substrate where sedimantation is most intense may be of selective value.

In summary, a critical problem which all marine invertebrates face is environmental unpredictability. This can be minimized by using cues where they are available to locate potential "refuges" from predictable hazards, but because no set of cues are reliable enough to predict all hazards, e.g., sedimentation, newly settled competitors and mobile micropredators, the morphological plasticity (Buss, 1979) and post-settlement reorientation ability of some colonial invertebrates can be a means of dealing with this unpredictability. Where growth form constrains the expression of morphological plasticity, such as in the determinately-growing Dendrobeania, other alternatives for responding to an unpredictable, changing environment should exist. In Dendrobeania, larvae use predictable cues such as light, shade, and specific substrate preferences to select micro-habitats as predicted by Buss (1979). The selective advantage of these microhabitats or "refuges" was hypothesized following the observation that colonies were smaller in "non-refuge" habitats, which were available to nudibranch predators. Colonies in "refuges" (worm tubes) were probably not available to the nudibranchs studied and were larger. After metamorphosis, the ability to reorient and elevate the ancestrula

via a rhizoid, may contribute to the competitive superiority (among colonial taxa) of Dendrobeania.

CHAPTER TWO

GROWTH, FECUNDITY AND LARVAL RECRUITMENT OF *DENDROBEANIA LICHENOIDES*

GROWTH, FECUNDITY, AND LARVAL RECRUITMENT OF *DENDROBEANIA LICHENOIDES*

INTRODUCTION

Reproductive output, age at maturity, and longevity, as well as other life history traits, interact to determine an organism's fitness (Stearns, 1977). One approach to life-history studies, (which assumes that energy is limiting), attempts to explain the relative apportionment of energy among various energy-consuming tasks such as reproduction, growth, and defense (Stearns, 1977). Sessile colonial invertebrates display a wide array of growth forms which appear to influence relative competitive ability and which presumably vary in their energetic cost (Buss, 1979, 1980; Jackson, 1979). It may therefore be possible to consider energy invested in defense-related growth form as a relative measure of the cost of defense. Jackson (1979) contrasted growth forms which represent a low commitment to maintaining occupied space (rapidly growing taxa, with simple morphologies) to those growth forms which represent a high commitment to spatial occupation (slowly growing taxa with complex morphologies), and made predictions about life-history characteristics associated with each. Successful space occupation was measured as the amount of space occupied and the relative ability to overgrow other taxa to procure space.

The predictions of Jackson (1979) are largely untested for many colonial invertebrates. Generalizations about longevity and other traits are confounded by difficulties in determining the life span or age of many colonial animals (Connell, 1973; Hughes and Jackson,

1980; Jackson and Winston, unpublished data); size is an inaccurate measurement of age because corals and tropical bryozoans can fuse to form large, young colonies or split to form small, old colonies (Hughes and Jackson, 1980; Jackson and Winston, unpublished data).

The literature on coral growth contains the best growth information available for colonial invertebrates (to date); a number of studies provide accurate age determinations, obtained by observing known colonies over time (Buddemeier and Kinzie, 1976; Connell, 1973; Glynn and Stewart, 1973) and support predictions about variations in growth rate and longevity with growth form (Buddemeier and Kinzie, 1976; Jackson, 1979).

In this chapter I present data on longevity, fecundity, and growth rate for a cheilostome bryozoan, Dendrobeania lichenoides. Dendrobeania has a plate-like growth form (a flattened, foliose form more or less parallel to the substratum and projecting into the water column from a limited zone of basal attachment [Jackson, 1979]), and consequently can be used as a model with which to test Jackson's (1979) predictions about life history traits of colonial invertebrates with plate-like morphology. He predicted that these will grow determinately (see definition for determinate in Chapter 1: fixed growth rate with a definite growth form), have a late time of first reproduction following an initial growth phase, a low fecundity, a high degree of polymorphism, special attachment roots, and a flexible skeleton. The plate-like morphology should be committed to survival within its area of settlement and therefore is expected to be a good competitor (Jackson,

1979).

MATERIALS AND METHODS

Growth and colony astogeny (budding pattern) were monitored for 12 colonies which settled as larvae in petri dishes in the laboratory on 27 December 1979, after which petri dishes were transplanted to the floating docks at F.H.L. and suspended in the water. Growth was directly measured each month as the number of zooids/colony until June 1980, when a photographic censusing method was developed. As a calibration to determine number of zooids photographically, 10 colonies were photographed, the prints of the colonies were cut out and weighed, and the number of zooids/gram of photograph was calculated (Fig. 6). Photographs of the 12 colonies were weighed, and using the calibration, the number of zooids/colony was calculated. Colonies were always photographed and printed at the same magnification and were printed on the same weight paper. Within 2 months, by August, 1980, colonies became too upright and foliose to permit estimation by this method. From August, 1980, petri dishes to which colonies were attached were weighed underwater (after scraping off all other epifauna and flora) to give a monthly estimate of growth. This method is adapted from the technique developed by Palmer (1980) to obtain growth measurements of live snails and largely measures the weight of skeletal material; the density of tissue is close to that of the water in which it is immersed and therefore registers a negligible weight (Palmer, 1980). Underwater weights were calibrated by weighing 5 colonies with a known number of zooids underwater (Fig. 6). This

method does not compensate for the differential weight of reproductive zooids with ovicells; thus, measurements of late summer and fall growth are slightly high (when each zooid is actually heavier because it has an ovicell), although probably not by more than 10 - 20 zooids. Error from other sources probably makes this negligible. Measurements of growth were terminated following the loss of several colonies in November 1980 and the partial degeneration of several others. After the growth monitoring was concluded, the weight of the petri dishes underwater was subtracted from the monthly measurements to give the actual colony weight underwater.

Fecundity was measured each month from August, 1979 to February, 1981 as the mean number of embryos/gram blotted wet weight (n= 5 colonies/month; embryos could be easily seen through the ovicell wall). Wet weights were regressed against dry weights to obtain a measure of wet weight variance (Fig. 7). Ethanol preserved colonies were dried in a 70°C oven until no further weight loss was recorded (1 - 2 days) to obtain dry weights. An inherent source of error in this technique is contributed by the seasonal regression of polyps and partial degeneration of colonies in the winter. Because colonies are not growing much and seem susceptible to tissue damage, they are carrying less somatic tissue in the winter relative to the summer. This means that if embryo number was not to change seasonally, the decrease in winter colony weight would probably result in a rise in the number of embryos/gram. The effect of this is a slightly inflated winter fecundity value, although qualitative seasonal changes should still be accurately measured.

Recruitment of larvae was monitored approximately bimonthly from July, 1980 to February, 1981. Four 10 x 10 cm plates were placed underneath the breakwater at F.H.L. adjacent to adult colonies every two months (approximately) and removed for censusing two months later. At each sampling date, all ancestrulae and colonies were counted on each of the four replicate plates with a Wild binocular dissecting microscope at 12x.

Quantity of larvae released from colonies was recorded while trying to obtain larvae for experimentation in August, 1979; September, 1979, 1980; October, 1979, 1980; November, 1980; December, 1979, 1980; February, 1981 and June, 1980 in the laboratory. Colonies were stimulated to release larvae by the established method of exposing colonies in running seawater to light after at least 8 hours of darkness (Reed, 1980).

To obtain some information about duration of brooding and time of recruitment, embryos were removed from ovicells at different times of the year and divided into two age classes: early cleavage (1 - 64 cells) or late stage embryos and larvae. All embryos were removed from 2 or 3 colonies and aged as early cleavage or late stage embryos and larvae in November, 1979; March, 1980; July, 1980 and August 1980.

RESULTS

Astogeny and Growth

The ancestrulae observed in the laboratory predictably produced a pair of buds (proximal and distal) at five to six days post-settlement, and each, in turn budded one or

two distal buds (Fig. 8a). Occasionally both proximal and distal sides continued growing to form a bilobed colony (Fig. 8b) or, more often, one side stopped and the other continued to grow, forming a mushroom-shaped leaf (Fig. 8c). In the field, both young colony types were found, although the majority of colonies were one-leaved. When the colony perimeter measured 360°, a second tier formed either by budding a new flap from the colony interior or by continuous growth at the lateral margins to form an overlapping layer supported by rhizoids, and attached to the lower tier. The attachment rhizoids which support the upper tier grew down from its underside and attached to the bottom level. In addition, two adjacent colonies can form a single complex by attaching together with rhizoids and were often couped in this way.

The plate-like growth form of Dendrobeania is variable and ranges from a small, rigid, tightly attached (with rhizoids), flat colony (Fig. 8c) to large, centrally attached, flexible fronds folded into an upright configuration (Fig. 1). Variation seems largely habitat dependent; colonies which occur intertidally are very small, flat encrustations. Subtidal colonies on vertical rock walls and overhangs at 30 to 60 feet are larger, slightly more foliose and less tightly encrusted to the substrate than those from the intertidal; their occurrence is very patchy, but they can occupy 60 to 90% of the cover where they occur. Underneath the breakwater at F.H.L., foliose upright colonies abound (Fig. 1), occupying up to 100% of the area in some 0.0625 m^2 quadrats. These colonies can be reduced to flat encrustations by nudibranch grazers which remove the upright edges, leaving only

the attached, central area (Chapter 3). It is possible, although speculative, that intertidal and subtidal colonies are subject to constant, heavy grazing and thus may never attain the foliose, folded growth form. It is also possible (and more probable) that the physical rigors of the intertidal such as desiccation and wave shock and other factors in the subtidal influence growth form. Reciprocal transplants and grazing experiments are necessary to clarify the nature of the variation in the growth form of Dendrobeania.

Dendrobeania's growth was geometric (as opposed to Gompertzian [Kaufmann, 1976]) like most other bryozoans studied (Bushnell, 1966; Dudley, 1973; Thorpe, 1979). The addition of zooids was very slow from settlement in December until May, after which it increased rapidly (Fig. 9). Colonies grew at a rate of about 40 zooids/month from January to May and at about 1,750 zooids/month from June to September, when over 2,000 zooids were added in a single month, Growth rate decreased in October. This cycle is representative of the cycle observed in field populations which grow very slowly in the late winter and spring following winter recruitment, very rapidly in the summer and fall, and die back in the winter.

Winter senescence in colonial invertebrates is poorly understood although it is common (Grave, 1930; Waters, 1966). In Dendrobeania, as in Bugula sp. (Grave, 1930), colonies regenerate vegetatively from colony fragments in the spring. It is not known for how many seasons the actual genome persists.

Fecundity

Fecundity (number of embryos/gram) was seasonal in Dendrobeania, with a maximum in October and November and a minimum in the early spring and summer (Fig. 10). Four months after settlement, winter-recruited colonies began producing embryos in May and June and continued egg production through February, when reproductive effort dropped off. The duration of brooding and numbers of eggs produced/zooid is unknown for Dendrobeania, although they were observed to produce at least 2 eggs/zooid. Other bryozoans have been recorded as brooding embryos for variable times, from 11 days to 4 months (Nielsen, 1981; Ryland, 1976; Stebbing, 1972) and passing as many as 4 embryos through each zooid in a season (Ryland, 1976).

The fecundity cycle was exaggerated by the winter decrease in somatic tissue; not only were there more embryos in winter colonies, but these colonies also had less somatic tissue than at the height of summer growth. The subsequent late winter - early spring decrease in fecundity was an accurate reflection of decreased reproductive effort in the colonies. In April, the degenerated colonies initiated new vegetative growth and were the only colonies which had embryos. The newly recruited winter colonies were still pre-reproductive. Once the newly recruited colonies became reproductive (June), these two different age classes of colonies became indistinguishable to casual observation. No attempt was made to distinguish them. The proportion of cleaving embryos/total embryos in a colony was measured to determine if embryos were produced all year round. In November, 1979, 12% (n=923) of the embryos removed from colonies

were early cleavage stages, 15% (n= 255) in March, 1980; 90% (n= 239) in July, 1980, and 41% (n= 260) in August, 1980, indicating that most embryos were produced in July, and in November very few embryos were produced.

Recruitment

In the process of trying to obtain larvae in the laboratory for experimentation, it was observed that larvae were released in great quantity from winter colonies (December, 1979; October - November, 1980), confirming that this was the time of peak release and recruitment. Very few larvae were released when colonies were stimulated by light in the summer, early fall or spring. Time of release may vary annually; there are reports of larval release of Dendrobeania in the laboratory in September (Reed, personal communication).

Recruitment panels showed larvae settling throughout the fall and early winter of 1980 (Table 4). Apparently larvae were recruiting in the field in small numbers even though there was very little larval release in the laboratory in late summer and early fall. The December to February decline in recruitment was much more abrupt than expected and could have been due to increased predation on settling larvae.

DISCUSSION

Dendrobeania, a relatively long-lived (1.5 years or more) temperate cheilostome, supports life history predictions made about colonial invertebrates with a plate-like growth form (Jackson, 1979). Dendrobeania has a relatively late time of first reproduction (4 - 5

Table 4. Mean number of Dendrobeania larvae recruited/month on styrofoam settling plates (n= 4 replicates/period).

	7/12/80-* 9/12/80	9/12/80- 11/11/80	11/11/80 12/8/80	12/8/80- 2/23/80
$\bar{x}$	59.5	106.7	77.2	6.8
s	37.1	22.6	55.4	6.4

* month/day/year

$\bar{x}$ mean

s standard deviation

months post-settlement) following a protracted initial growth phase. Relative fecundity is difficult to assess due to the paucity of comparative data and problems in its measurement (seasonal variation in somatic tissue), but the relatively long brooding time (maybe up to 2 months) and seasonally large proportion of non-reproductive tissue (see also Chapter 3) suggests a low fecundity/time relative to short-lived bryozoa in which most zooids of the colony can produce a mature larva every 2 - 4 weeks (Correa, 1948; Ryland, 1976). As predicted for a plate-like morphology, Dendrobeania seems well adapted to maintain space once it has settled; initial growth before reproduction ensures the occupation of available space, and defensive spines, attachment rhizoids, and other attributes maintain space against predators and competitors (Chapter 1, Chapter 3). The competitive dominance (Chapter 1) and skeletal flexibility of the upraised colony also conform to the predictions of Jackson (1979), suggesting that it may be possible to draw general conclusions about life history attributes from the morphology of colonial invertebrates.

Growth and reproduction in most temperate invertebrates varies seasonally correlated with changes in day length and temperature (Elven, 1976; Spight, 1979; Eggleston, 1972). Long-lived bryozoans are generally dormant during winter periods of low temperature and short day length and grow predominantly during summer periods (Eggleston, 1972; Gordon, 1970; Grave, 1930; Stebbing, 1971). Most researchers have concluded that short day length is more important limiting bryozoan seasonal growth than temperature because of its effect on phytoplankton standing crop (Gordon, 1970; Eggleston, 1972),

although in cold temperate latitudes temperature may also be a factor (Abbott, 1973; Eggleston, 1972). In the Pacific Northwest, where water temperature only varies 4 or 5°C seasonally, the extreme reduction in day length from approximately 16 hours of light/day in the summer to about 8 hours of light/day in the winter (personal observation) causing a phytoplankton decline, is probably the major factor limiting growth of Dendrobeania. Growth slows in October at a time when day length is shortening considerably (and therefore phytoplankton is declining), but temperature has only dropped 2°C (Fig 11). Spring growth increases with increasing day length (and therefore phytoplankton production) before temperature shows much change.

The fecundity and recruitment of Dendrobeania peaked in late fall and early winter. Most algae and invertebrates recruit in the spring and summer so this is somewhat anomalous, although a number of other bryozoans recruit in the winter (Abbott, 1973; Eggleston, 1972; Gordon, 1970). Paine and Levin (1981) noted that winter recruitment was required of species which recruit into disturbance-created patches in mussel beds; more and larger patches are created in the winter due to storms, and mussels (Mytilus californianus) do not recruit until spring, thus competitive subordinates can best invade by winter recruitment. In addition, predators in the mussel bed were less active in the winter (Suchanek, 1978). Winter recruitment is also a seemingly good strategy for other organisms which live in space-limited habitats because considerable space can be freed by winter mortality of seasonally abundant algae and colonial invertebrates, and in addition, the activity of some predators is reduced (Chapter 3).

Eggleston (1972) studied life cycles and reproductive patterns of common Manx (England) bryozoans. He concluded that there were three life history patterns based on colony longevity: 1) short-lived (sub-annual), 2) annual, and 3) perennial taxa. In general, the number of embryo-bearing individuals and the size and development of larvae was proportional to colony longevity. Eggleston noted that sub-annual bryozoans grew and reproduced early; this has been confirmed by later studies (Dudley, 1973; Yoshioka, 1973). Many of these sub-annuals free-spawn (therefore do not brood) and possess few colony specializations or polymorphosms. Annual taxa grew and reproduced at a much slower rate than sub-annuals (Eggleston, 1972). Perennials were less seasonal than annuals in growth and reproduction, but usually passed part of the year in a dormant phase as degenerate colonies. Dendrobeania, which lives at least one and a half years (and probably longer), conforms to Eggleston's perennial category.

In summary, this study suggests that it may be possible to draw general conclusions about life history attributes from the morphology of colonial invertebrates as predicted by Jackson (1979). Dendrobeania has a consistent, although variable plate-like morphology which conforms to the predictions of Jackson (1979) for plate-like colonial invertebrates. Dendrobeania also shares life history characteristics with perennial bryozoans as described by Eggleston (1972).

CHAPTER THREE

THE ROLE OF INTRA-COLONY VARIATION IN LIMITING THE EXTENT OF NUDIBRANCH PREDATION

THE ROLE OF INTRA-COLONY VARIATION IN LIMITING THE EXTENT OF NUDIBRANCH PREDATION

INTRODUCTION

The role of prey defense in the predator-prey interactions of sessile, colonial marine invertebrates and their consumers is poorly understood. In most cases, colonial animals are grazed by some predator despite chemical and morphological defenses, but often each colony is only partially consumed and the remaining tissue can regenerate (Birkeland and Gregory, 1975; Bayer, 1963; Wahle, MS). This situation is analogous to the relationship between plants and their herbivores and raises the question of what prevents entire colonies from being consumed. In many cases it should be energetically more profitable for a grazer to remain and consume an entire colony rather than leave it partially unconsumed and forage elsewhere (Birkeland and Gregory, 1975).

Colonial invertebrates exhibit numerous parallels with plants because they both are constructed of semi-autonomous units which can regenerate if damaged (Harper, 1977; Harper and Bell, 1979). Because the theory of plant-grazer interactions is well-developed relative to that of invertebrate-grazer interactions, it is profitable to apply the former theory to invertebrate colonies and their grazers. The role of plant defenses in limiting consumer population densities has only recently been recognized (Haukioja, 1980). In contrast, previous authors suggested that herbivores are limited only by higher order predators, rather than by their resources (Hairston, Smith, and Slobodkin, 1960). This point of view was contested by Murdoch (1966)

and Ehrlich and Birch (1967), who cited cases of plant defense limiting individual herbivores. The importance of age-related secondary compounds, induced and intra-plant heterogeneity of defense in limiting the extent of herbivore damage has also been demonstrated (Haukioja, 1980; Rhoades and Cates, 1976; Whitham, in press; cf Janzen, 1979), revealing that herbivores frequently can harvest only certain non-defended portions of their resource or only consume them at certain times, allowing the remainder to regenerate (from herbivore damage).

Known defenses of colonial animals range from structural features, e.g., heavy calcification (scleractinian corals and bryozoans) and spicules (sponges) to chemical deterrents, e.g., acid and vanadium secreting cells in tunicates (Stoecker, 1980) and mechanical devices, e.g., nematocysts (scleractinian corals, hydrozoans, and scyphozoans). Spines, which are common on scleractinian corals and bryozoans, are probably largely defensive (Stebbing, 1973; Yoshioka, 1973). Yoshioka (1973) reported that spines were induced on Membranipora serrilamella in response to grazing by a nudibranch. The nudibranch consumed single polyps of M. serrilamella by forming a seal over the frontal membrane and sucking out the zooecial contents. Induced spines reportedly prevented the nudibranch from forming an effective seal (Yoshioka, 1973).

Considerable information about morphological and chemical defenses of entire invertebrate colonies is available (Bakus, 1981; Jackson and Buss, 1975; Stoecker, 1980), but very little is known of the intra-colonial arrangement of defensive units which might affect grazers. Intra-resource heterogeneity (between leaves on a tree, and within a leaf)

is believed to play an important role in reducing the extent of plant damage caused by herbivores (Whitham, in press). Asexually proliferating colonial invertebrates share many demographic and growth features with plants (Harper and Bell, 1979) and may have similar defense mechanisms against grazers.

Dendrobeania lichenoides, a foliose, anascan bryozoan, is grazed by three nudibranch species which rarely consume an entire colony, but instead graze the outer edges of a number of colonies. It appears that the grazing pattern is controlled by some characteristic of the colony because the pattern is fairly consistent over a number of colonies for different species of nudibranch. This suggests that there is a consistent intra-colonial arrangement of materials or structures which varies within the colony and limits the extent of nudibranch grazing. This chapter documents intracolonial variation in morphology and function, e.g., relative calcium carbonate content, relative regenerative ability, numbers of brown bodies and positioning of rhizoids. It also explores intracolonial differences in palatability and attempts to isolate which factors could limit the extent of grazing on Dendrobeania by nudibranch predators.

MATERIALS AND METHODS

All Dendrobeania colonies were collected underneath the breakwater at Friday Harbor Laboratories (F.H.L.), Friday Harbor, Washington, U.S.A. using SCUBA (self-contained underwater breathing apparatus). Colonies were carefully collected by severing attaching rhizoids with a razor blade, after which intact colonies could easily be removed from

the substrate. Most field observations were made underneath the breakwater in addition to subtidal observations made at Point George on the southwest side of Shaw Island and at a site north of Turn Island (Fig. 2). Intertidal observations were made at Pile Point on the southwest side of San Juan Island and at Bamfield Inlet, Bamfield on Vancouver Island, British Columbia (Fig. 2).

Intra-Colony Zonation and Gradients

Alternating dark and light bands across the colony, probably representing morphological zonation, were apparent on all Dendrobeania colonies. Morphological features contributing to the banding were quantitatively examined in August, 1980; all measurements were made with an ocular micrometer at 12x. This sample represents one point in time; zones will change in absolute and relative size with colony growth. For example, the eggs will occupy a greater proportion of the colony with increasing age. Eight different parameters were selected because of their potential importance to colony function and in affecting predation by nudibranchs. The parameters are as follows (see Fig. 12):: 1) Maximum number of brown bodies: this variable is the greatest number of brown bodies found in any one zooecium in the colony. A brown body is the waste product of a degenerated polypide (Hyman, 1954). The number of brown bodies is a rough estimate of colony age; older colonies have undergone more degeneration-regeneration cycles and thus have more brown bodies in their oldest zooecia (Gordon, 1977; Palumbi and Jackson, MS). 2) Colony size: length x width of the entire colony. Although the roughly circular colonies vary in their linear dimensions, this

was believed to be the best simple size approximation. 3) Spineless margin: the budding edge with undifferentiated and partially differentiated zooids. Most zooecia in the colony have ovicells and spines, however these have not yet formed in this zone. The spineless margin is unprotected relative to other regions of the colony. 4) Distance from the first brown body to the edge: the first zone of degeneration proximal to the budding edge is marked by zooecia containing one brown body. This is of functional interest for at least two reasons: a) because most of the polypides have not yet regenerated and so the zooecia are non-feeding, and b) because this zone marks the beginning of an intra-colonial aging process (about which little is known [Gordon, 1977]). 5) Distance from the first oocyte to the edge: continuing on an ontogenetic gradient of increasing age from the margin, these are the first zooecia in which reproductive products are visible. Oocytes are bright orange and can be seen through the transparent frontal membrane. When mature, the eggs move into the ovicells and are fertilized (Silen, 1954). The process by which this occurs is not well understood. 6) Distance from the first rhizoid to the edge: rhizoids grow down from the undersurface of the colony and adhere to the substrate (Fig. 12). Measurements of their first occurrence relative to the edge is very variable -- most appear at about the same distance as first oocytes, but sometimes there are rhizoids in the first brown body zone. 7) Distance from the first embryo in an ovicell to the edge: the beginning of the mature, embryo-bearing region of the colony. 8) Width of embryo zone: the broad band in the center of the colony containing embryos (cleaving eggs to mature larvae). This area is easily dis-

tinguished by the presence of orange eggs in translucent ovicells.

The measurements 3 through 7 are taken as the length of a line perpendicular to and beginning at the colony budding edge and ending at the beginning of the specified zone (Fig. 12). Five replicates of each measurement were taken per colony. Four parameters (number of brown bodies, oocyte to edge, rhizoid to edge, and embryo width) were subsequently compared to colony diameter by correlation analysis; rhizoid distance and oocyte distance were compared to each other with correlation analysis (Sokal and Rohlf, 1969). After determining that the variances were homogeneous, a two-way analysis of variance (ANOVA) with replication was run on the same two characters (rhizoid, oocyte) to analyze the importance of between and within colony variance (Sokal and Rohlf, 1969). Most statistical analyses were performed with Michigan Interactive Data Analysis (MIDAS) packages (Fox and Guire, 1976); the two-way ANOVA was run on APL.

Besides the apparent intra-colony morphological zonation, there are less obvious gradients, which are potentially important to predators. The proportion of $CaCO_3$/total tissue was measured in three different regions of the colony. Strips of approximately 0.5 x 3.0 cm were cut from 1) the spineless margin, 2) the two brown body zone, and 3) the three or more brown body zone. All pieces were rinsed in 70% ethanol and subsequently dried in a 70°C oven until there was no further weight change and then final weights were recorded. Dried colonies were placed in a muffle furnace and incinerated for 24 hours at 1500°C. The weight after this treatment approximates the weight of the inorganic $CaCO_3$ skeleton. The ratio of the incinerated weight to the total dry weight is a measure of the proportion of $CaCO_3$ in each part of the

colony tested.

In August, 1980, intra-colony regeneration rates were measured in the field, using the method of Jackson and Palumbi (1980). Holes were bored in the margins of eight colonies and in the centers (inner embryo region) of eight others with a 4 mm cork borer. The time to regeneration of the colonies was monitored.

Predation

Predator surveys were conducted 4 times: August, 1980; October, 1980; December, 1980; and February, 1981. At these times all nudibranchs of 3 species (Triopha catalinae: Doridaceae; Dirona albolineata, D. aurantia: Arminaceae) on the entire study area (breakwater) that were large enough to be seen from 1.5 meters away were counted. This method reliably locates all the nudibranchs in the size class (3 - 20 cm) in which I was interested.

Seasonal variation in the number of nudibranch-grazed colonies was measured in August, 1980 and October, 1980. Colonies grazed by nudibranchs were obvious because of their ragged, serrated margins which were identical to those of Dendrobeania grazed in the laboratory. Three transects were randomly positioned from on top of the breakwater by attaching one end of a 12 meter line to the dock and positioning the other end with a float from under the breakwater. The total number of grazed and ungrazed colonies within approximately 0.5 meters of the 10 meter long transect were counted.

Consumption rates of nudibranchs on colonies were measured in the laboratory using two methods: the time taken for a nudibranch to consume an entire colony and the weight loss of grazed colonies over a standard

time increment. Underwater weights were used for the latter method to minimize stress on colonies prior to grazing, and were obtained by suspending colonies from the suspension hook underneath a Mettler p-163 balance into a beaker containing 11-12°C seawater. Live colonies were weighed underwater, fed to nudibranchs (Triopha catalinae, Dirona aurantia) and the remainder weighed underwater. Control colonies were weighed initially and after the experiment to control for any metabolic weight changes. Because the mean weight change of 4 control colonies was 0.008 gm, the weight change was considered negligible. The actual weight recorded is proportional to the weight of the skeleton, because tissue is close to the density of water and registers a negligible weight (Palmer, 1980). The regression of number of zooids against underwater weight as calculated in Chapter 2 is: $Y= 49632.0X + 366.7$, $r= 0.983$.

The relationship between prey density and percent colony consumed was examined by varying prey density (number of colonies) in laboratory feeding experiments. Colonies of similar size were individually weighed underwater and placed in 1/4" mesh VEXAR net aquaria with running seawater in densities of 1, 2, 3, 4, and 5 colonies. Control colonies in the seawater table were weighed before and after each experiment to control for metabolic weight changes, although this was considered negligible because the mean weight change of the 8 controls was 0.007 gm. Because of the variance in weight/colony, results were analyzed by number of colonies/trial and total weight of bryozoan/trial, although there is a good correlation between number of colonies and total weight: $Y= 0.151X - 0.006$, $r= 0.901$. Trials were run in groups of two or

three densities, with always at least one treatment of density one. One arminacean nudibranch (Dirona albolineata; D. aurantia) was added to each cage and allowed to feed until the single colony treatment was entirely consumed. This was the only way to standardize differences in nudibranch consumption rates. Values were log transformed to generate a linear relationship and a regression line was calculated between log %colony consumed and log colony number.

Intra-colonial palatability differences were examined in the laboratory. Pieces were cut from 4 regions of each colony: 1) spineless margin, 2) one brown body, 3) two brown body, and 4) three or more brown body. Each region was replicated 4 times and epoxied in a latin square configuration to a glass plate. "Z-spar" marine epoxy was used as an adhesive (Whittaker, Corp., Costa Mesa, California). Each of four replicate plates was placed in a sea water table with a small Dirona albolineata (3 cm long) and left for 8 - 10 hours. The same nudibranch was used for 3 trials, a slightly larger one was used for the fourth trial. Results were analyzed with an ANOVA after determining that the variances were homogeneous with a F-max test (Sokal and Rohlf, 1969). The difference between means was tested with a Scheffés test (Fox and Guire, 1976).

The effect of rhizoids on nudibranch grazing was observed in the field and the laboratory. Underneath the breakwater, rhizoids were severed on all colonies (at least 20 colonies/plot) in two 0.0625 m^2 plots. A Triopha catalinae was introduced to each plot and a 1/4" VEXAR mesh cage placed over the plot. The cage was secured in place by the buoyancy provided from styrofoam side supports which floated it

tightly up against the breakwater underside. T. catalinae were also added to two controls of Dendrobeania with intact rhizoids and an identical VEXAR cage. After two weeks, the cages were removed and results qualitatively observed. Attempts to quantify the results by underwater photography were unsuccessful.

In the laboratory, two T. catalinae were offered four colonies attached to Styela gibbsii with intact rhizoids and four with severed rhizoids. Colonies were left for 48 hours and then observed. No attempt was made to quantify observations.

RESULTS

Intra-colony Zonation and Gradients

The light and dark banding visible on Dendrobeania colonies represent intra-colonial division into different functional regions. Figure 12, summarizing data from Table 5, depicts the zones and their spatial relationships. In addition, the inset is a profile of the colony in longitudinal section, displaying the location of rhizoids. The mean distances from the margin of the colony to the beginning of each zone is indicated in Figure 12. Because some of these distances appeared to vary with colony size, they were compared over all colonies to colony size with correlation analysis (Table 6). Number of brown bodies and embryo zone width were significantly correlated with colony size at $p < 0.001$. The oocyte and rhizoid measurements were not correlated with colony size, but were significantly correlated with each other ($p < 0.01$). A two way mixed model ANOVA, run on oocyte and rhizoid distances to examine within and between colony variability

Table 5. Morphological parameters of Dendrobeania colonies. Each value is a mean (with standard deviation in parantheses) of 5 replicate measurements taken for each colony.*

Colony number	Number of BB	Oocyte to margin	Rhizoid to margin	Embryo width	Diameter (LxW)
1	--	7.41 (1.08)	9.18 (2.19)	10.41 (0.42)	810
2	--	8.54 (0.46)	6.56 (1.59)	8.70 (2.73)	682
3	--	6.56 (0.62)	8.16 (3.72)	6.80 (1.96)	686
4	1	5.10 (0.96)	5.84 (0.50)	8.30 (4.04)	920
5	3	7.96 (1.20)	7.60 (1.52)	19.80 (0.45)	1200
6	2	7.10 (0.65)	3.60 (0.65)	6.60 (0.89)	561
7	1	8.28 (0.91)	9.80 (0.84)	7.80 (1.04)	651
8	1	5.50 (0.21)	4.30 (1.99)	7.10 (0.65)	525
9	1	4.90 (0.82)	3.84 (0.59)	6.20 (0.27)	493
10	2	7.30 (0.84)	2.90 (0.74)	15.40 (1.19)	630
11	2	6.60 (1.52)	6.56 (1.67)	6.20 (2.20)	540
12	2	5.66 (0.48)	9.00 (1.00)	12.20 (2.39)	546
13	3	6.00 (1.22)	7.82 (1.68)	14.20 (2.28)	722
14	3	4.30 (0.76)	2.80 (1.09)	15.00 (2.83)	1120
15	3	5.40 (1.63)	2.81 (0.76)	17.62 (0.55)	800
16	1	--	5.32 (1.30)	4.10 (0.22)	360
17	4	6.22 (0.63)	--	23.80 (4.15)	1200
18	3	6.30 (1.44)	4.40 (1.98)	18.00 (0.71)	1008
19	2	8.50 (1.46)	3.50 (1.22)	9.70 (1.35)	495
20	4	6.00 (0.71)	7.06 (2.16)	14.40 (2.07)	1075
21	2	6.94 (0.44)	4.50 (1.32)	9.40 (0.82)	425
22	2	--	--	16.41 (1.52)	672

-- no sample taken

* measurements are in micrometer units (0.076 x mic. unit= cm)

BB brown body

Table 6. Correlation analysis on morphological parameters of *Dendrobeania* colonies. In each row of the table, the product-moment correlation coefficient describes the degree of correlation between the two parameters listed in that row.

Parameter 1		Parameter 2	Significance level
log # brown bodies	(n= 19)[1]	log colony size	r= 0.647 ***
log oocyte distance	(n= 20)	log colony size	r= -0.155 ns
log rhizoid distance	(n= 20)	log colony size	r= 0.083 ns
embryo width	(n= 22)	log colony size	r= 0.727 ***
log rhizoid distance	(n= 20)	log oocyte distance	r= 0.291 **

** $p<0.01$

*** $p<0.001$

ns not significant at $p<0.05$

1 number of colonies on which each parameter was measured; 5 replicates/colony.

confirmed that there was no significant difference between the distance from the margin to the beginning of the oocyte or rhizoid zone, and in addition, there was no significant difference among replicate measurements within a colony (Table 7). The variation was largely explained by an among-colony component, which we know is not a consistent variation with size because neither of these variables was correlated with size. A significant interaction term can probably be explained by the large among-colony variation in stolon distance relative to the less variable oocyte distance (Table 5). Although the mean distance from the margin to the beginning of both the rhizoid and oocyte "zones" was similar, the actual distribution was not the same: rhizoids occurred distal (closer to the margin) or proximal to the more constant oocyte zone. Rhizoids did not become predictably present and abundant until the embryo zone; distal to this, where they were measured, they were scattered and unpredictable.

Calcium carbonate/total dry weight varied between the margin and two brown body regions in the colony (Table 8). The difference between the relative $CaCO_3$ in the 2 brown body and in the colony interior (3 or more brown body) seemed negligible.

Regeneration rates also varied within a colony. Holes bored near the growing edge regenerated within a month in the summer (n= 8 colonies). Inner colony regions (embryo) did not regenerate in 5 months (n= 7 colonies, one colony was lost).

Predation

Dendrobeania colonies were heavily grazed in the field by the nudibranchs Triopha catalinae, Dirona albolineata, and D. aurantia. In

Table 7. Mixed model 2-way ANOVA (with replication), analyzing between and within colony variance in stolon and oocyte distances from the margin (n= 20 colonies)*

Source of variation	df	SS	MS	F
Between variables (stolon and oocyte)	1	33.048	33.048	2.07'ns
Among colonies	19	510.918	26.890	19.41***
Interaction	19	249.358	13.124	7.63***
Error (between replicates)	160	275.470	1.721	
Total	199	1068.801	5.371	

* variances are homoscedastic, stolon/oocyte= 7.169/4.059= 1.766 (ns)

*** $p<0.001$

' because this is the fixed variable in a mixed model (a random and a fixed treatment) ANOVA with a significant interaction term, F is calculated as MS variable/MS interaction.

Table 8. Proportion of ashed/total dry weight ($CaCO_3$/total dry weight) in margin, 2 brown body and 3 brown body regions of Dendrobeania colonies (n= 5 colonies/replicate).

Replicate	Margin	2 Brown Body	3 or More Brown Body
#1	0.69	0.76	0.79
#2	0.51	0.76	0.77

August and October, 1980, 41% (n= 177) and 58% (n= 571) of all colonies examined showed clear evidence of grazing.

Laboratory experiments revealed very high consumption rates by Triopha catalinae and D. albolineata. T. catalinae consumed a 3 cm colony in 10 minutes and on a separate occasion, consumed colonies at a mean rate of 968 ± 132 zooids/hour (n= 2). D. albolineata averaged 729 ± 270 zooids/hour (n= 6) in feeding trials. No attempt was made to examine changes in feeding rate with predator size.

In the field, colonies in heavily grazed areas were cropped closer to the substrate, than those in less heavily grazed areas. In the laboratory, there was a clear relationship of decreasing %colony consumed with increasing number of colonies (or total weight): r= 1.93 - 0.84X (Table 9, Fig. 13). This is because nudibranchs were eating around the outer edges of colonies when prey were abundant, but consumed more of each colony when less prey were available. This suggests that the margin area of the colony is preferred.

Field and laboratory observations of colonies with severed rhizoids revealed that more of each colony was consumed if rhizoids were severed. Attempts to quantify this observation with underwater photographic equipment were largely unsuccessful. In most cases, the attached central area of the colony remained if stolons were intact, but was occasionally removed (consumed) if stolons were severed. Both field and laboratory experiments were run with relatively few colonies/nudibranch and confined nudibranchs. This represents a severe grazing condition relative to some natural conditions, although high Triopha catalinae densities on populations of Dendrobeania have been observed subtidally (Best and Emlet, pers. com.; personal observation).

Table 9. Percent of each Dendrobeania consumed by Dirona albolineata and D. aurantia as a function of the total weight of colonies offered in each trial.

% consumed/gm	Number of colonies	Weight of colonies (mean)
90	1	0.188
100	1	0.141
92	1	0.213
43	2	0.171
28	2	0.120
59	3	0.122
57	3	0.072
15	3	0.168
17	4	0.173
33	5	0.161

In the palatability experiment, D. albolineata did not consume colony pieces from the 3 brown body zone, but ate most pieces from the 0, 1, and 2 brown body zones ($p<0.001$; Tables 10,-11).

DISCUSSION

The three nudibranch species examined consistently ate around the perimeter of Dendrobeania colonies and left the inner colony regions largely unconsumed. Because they are located in the inner colony, zooids containing mature reproductive products (embryos) were consumed less than other zooids. Since colony fitness is proportional to the number of larvae produced (Ryland, 1977), this grazing pattern would be less damaging than one which included reproductive products.

Differential nudibranch consumption of cut-out colony portions demonstrates that intra-colony palatability differences are independent of overall colony morphology. Rejection of portions only from the center of the colony suggests that some trait associated with this area is distasteful to nudibranchs. Those traits which increased toward the center of the colony, relative to the margin, and which may limit the extent to which a colony is grazed are: 1) $CaCO_3$/total tissue, 2) rhizoids, and 3) brown body number. In addition, regenerative ability varies from the margin to the center and may have an associated chemical gradient which affects palatability. The only portion left unconsumed in the palatability trial was the 3 brown body region, within which the predator-deterrent factor would appear to be most effective.

The ratio of $CaCO_3$/total tissue is as high in the second brown body as in the third brown body region. Thus it seems unlikely that this factor alone is limiting the level in the colony to which nudi-

Table 10. Number of Dendrobeania colony pieces remaining after 8 hours exposure to Dirona albolineata grazing. Number of pieces offered each trial = 4.

Trial #	0 Brown Body	1 Brown Body	2 Brown Body	3 Brown Body
1	0	0	0.5	3
2	1	0	0	4
3	1	2	0.5	3.5
4	0.5	0	0.5	2

Table 11. Analysis of variance testing for intra-colonial differences in palatability of Dendrobeania to Dirona albolineata.

Source of variation	df	SS	MS	F
Between treatments	3	27.422	9.141	19.286***
Within treatments	12	5.687	0.474	
Total	15	33.109		

Scheffes difference between means

	0BB[1]	1BB	2BB	3BB
		***		

1 BB - Brown Body

*** significant at $p < 0.001$

branchs graze. The palatability experiment also excludes rhizoids from consideration because they first appear in the two brown body zone which is readily consumed. However, I feel that the rhizoids are not effective as deterrents until they are dense and tightly attached to the substrate, as in older regions of the colony. Rhizoids are clearly not the factor which normally limits predation to the outer margins, because grazing usually stops before the area where the rhizoids could be really effective, but they appear to be effective when grazing is heavy. Under the latter circumstances, only the very central portion of the colony, (which adheres tightly to the substrate) remains. This apparently occurs because of the difficulty with which these nudibranchs manipulate encrusted colony portions. In California, Triopha catalinae primarily ate erect bryozoans while a congener T. maculata, with a narrower radula, ate both encrusting and erect bryoaons (Nybakken and McDonald, 1981). It may be that T. catalinae's broader radula is inefficient at rasping off encrusted colony regions (Nybakken and McDonald, 1981).

Comparisons (using SCUBA) of control plots with plots containing experimentally severed rhizoids and introduced nudibranchs provide a qualitative test of rhizoid importance in limiting nudibranch grazing under severe grazing conditions. Although quantitative data are unavailable, those plots without rhizoids appeared more completely grazed than those with rhizoids within two weeks of nudibranch introduction. Laboratory observations confirmed that colonies without rhizoids were consumed faster and more completely than colonies with rhizoids.

Age-related intra-colony variation in regeneration rate suggests that there are physiological gradients within Dendrobeania. Physiological gradients have been described in other cheilostome and ctenostome bryozoans examined (Bronstein, 1939; Gordon, 1968; Zirpolo, 1924; Palumbi and Jackson, MS), which also exhibit very little or no regenerative ability in the center of the colony (Bronstein, 1939; Palumbi and Jackson, MS). Bronstein (1939) related variations in intra-colonial regenerative ability to a physiological gradient which was marked by a change in the refractive index of the coelomic fluid between old and young zooids. He thought that the decreased refractive index in older zooids reflected decreased colloidal protein. The presence of an undefined, age-related physiological gradient could easily cause a change in palatability.

The pattern of feeding by nudibranchs on Dendrobeania is best explained by increased brown body number and stolons in the inner colony region. Preliminary chemical analyses reveal that brown bodies, the product of degenerated polypides, have a higher nitrogen/carbon ratio than whole colonies. In addition, there is twice as much ninhydrin reactive material (amino acids) in brown bodies as in the parent colony (Lipson and Schopf, unpublished data). Other than this, there is little evidence on which to speculate about the mechanism by which brown bodies could decrease palatability. They clearly are not strongly toxic as small quantities are readily consumed with younger portions of the colony. It is possible that the large amino acid component contains digestibility-reducing compounds, e.g., proteinase inhibiting non-protein amino acids which are seen in many plants (Rhoads and Cates, 1976). It is also possible that some unknown

factor co-occurs with the three brown body zone and confers distastefulness.

Are Partial Predators "Prudent" Predators?

Central to the entire discussion of predation on colonial organisms is the phenomenon of partial predation (grazing) as opposed to whole organism predation. Partial predation raises two problems: 1) why does the predator not consume the entire resource, and 2) why do organisms that have the capability to regionally limit grazing not defend the entire colony, particularly if there is no advantage to being grazed (but see Owen and Wiegert, 1980)? The first question is discussed below; in answer to the second, plant defense theory predicts (Janzen, 1979) that a resource should only evolve a defense against grazers which is cost-effective, e.g., a crop pest should be reduced in density only to the point where its effects are just slightly greater than the cost of getting rid of it. "One doesn't pay $21.00/acre to get rid of a pest that damages $3.00 worth of crops/acre, but one might pay $2.95/acre to remove it" (Janzen, 1979).

Induced or partial defenses of some colonial animals could explain why the entire colony isn't consumed or the "prudent predator" phenomenon. The term "prudent predator" was coined to describe the efficiency with which some predators use their prey, e.g., consuming prey of low reproductive value, not depleting an entire prey population, etc. (Slobodkin, 1961, 1968, 1974). Evolutionarily, prudent predation must be explained as the prey evolving escapes that limit the predator rather than as the predator abstaining from over-exploiting a resource;

the latter requires group selection to occur (Slobodkin, 1974; Maynard-Smith and Slatkin, 1973).

The three nudibranchs grazing Dendrobeania are all "prudent" predators in the sense that they largely consume non-reproductive tissue (although not exclusively) and leave their resource to regenerate for another meal. This behavior may be explicable in terms of the selective pressure on colony design to produce traits which limit the extent of damage to each colony. Two general traits which might enhance the "prudence" of predators on colonial invertebrates are: 1) the positioning of reproductive elements behind a chemical or morphological barrier to grazing, and 2) the limitation of grazers to new, rapidly regenerateable, non-reproductive tissue or old post-reproductive tissue. There is some evidence for these suggestions; bryozoan ovicells are calcium carbonate shells in which embryos are encased from the time of fertilization until larval release and represent a case of specific protection for reproductive tissue; some coral grazers consume mostly young, rapidly regenerateable, non-reproductive tissue (Birkeland and Gregory, 1975; Wahle, MS). Birkeland and Gregory (1975), in a study of Cyphoma gibbosum (prosobranch gastropod) predation on gorgonian corals, noted that C. gibbosum was a "prudent" predator, consuming only parts of colonies and then moving on to others. This behavior seemed energetically expensive, and could not be explained satisfactorily without invoking group selection, unless the presence of induced defense in the prey such as postulated for Membranipora serrilamella (Yoshioka, 1973) or simply intra-colonial variation in resource quality were invoked.

Consistent intra-colonial variation in the position of brown bodies, rhizoids, and reproductive products in Dendrobeania are suggested as adaptations to nudibranch predation, although other selective pressures may affect these traits. Experiments showed that inner colony regions containing reproductive products and brown bodies were less palatable to grazing nudibranchs than outer colony regions, probably explaining why they were rarely consumed in the field. In addition, inner colony regions attached to the substrate by rhizoids appeared inaccessible to some nudibranch grazers.

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FIGURES

Figure 1. Dendrobeania colony at the height of summer growth accompanied by a nudibranch predator, Dirona aurantia. This upright variation of the normally recumbent colony is accomplished by folding and contorting into an upright shape, and is maintained by growth and attachment of rhizoids from one frond to another.

scale= 2 cm.

Figure 2. Study sites in the San Juan Archipelago and on Vancouver Island, British Columbia.

1- Point George
2- Turn Island
3- Rosario
4- Pile Point
5- Bamfield Inlet, Bamfield, B.C., Canada.

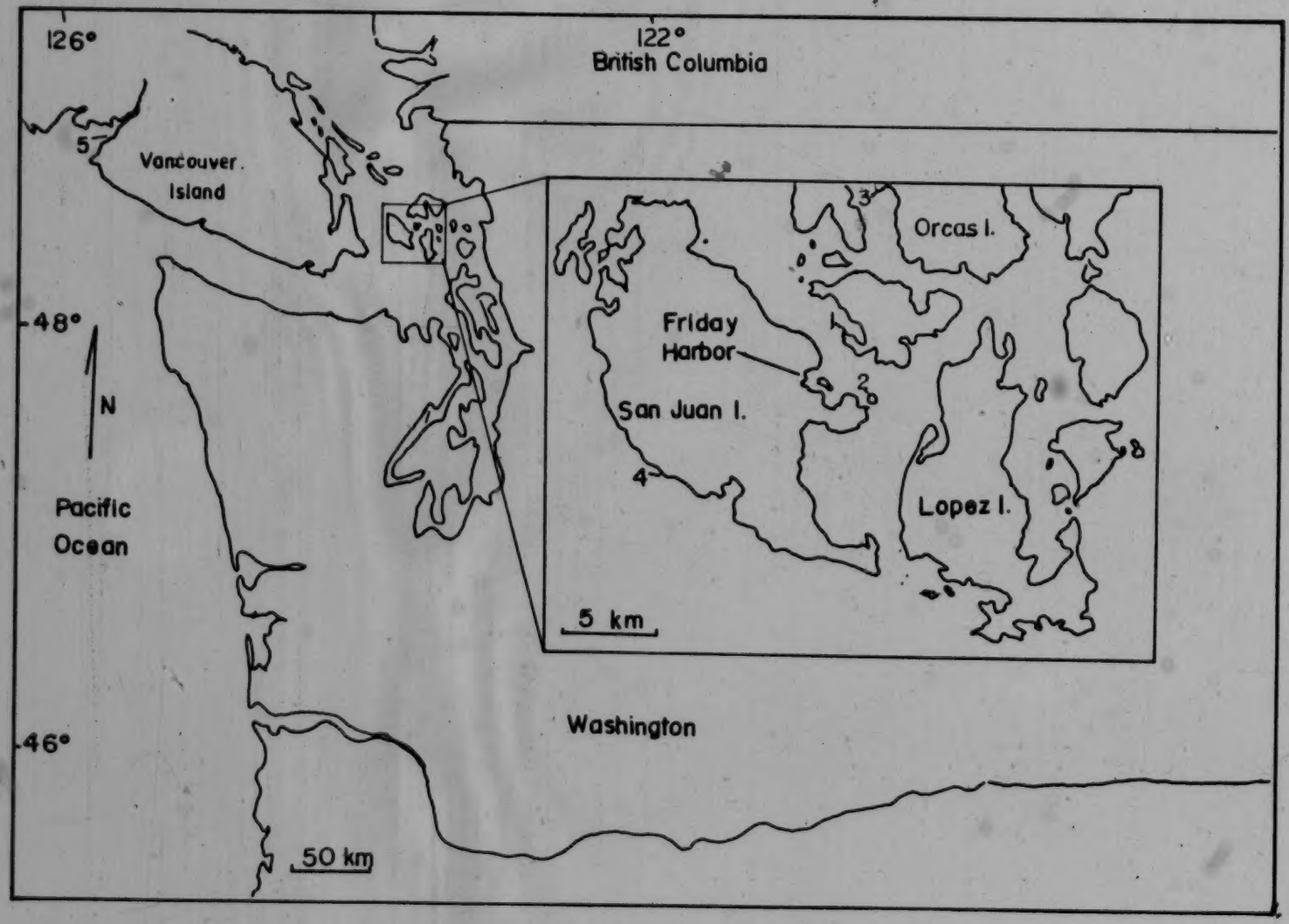
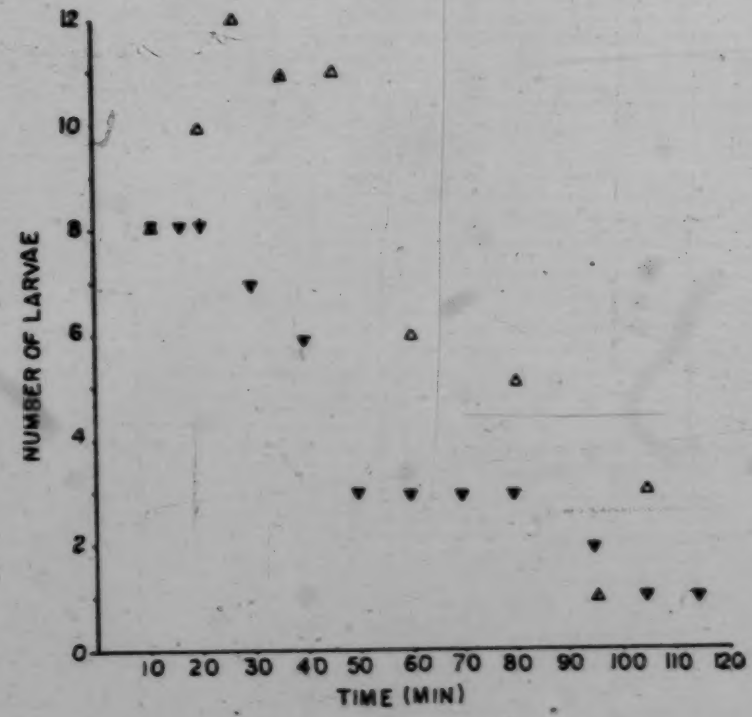
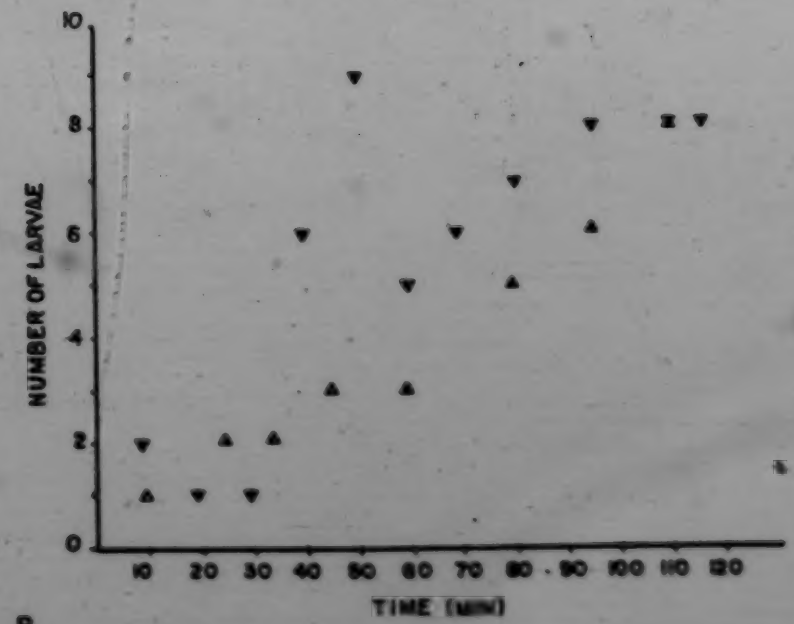

126°
122°
British Columbia
5
Vancouver
Island
48°
N
Pacific
Ocean
Orcas I.
3
Friday
Harbor
1
San Juan I.
2
4
Lopez I.
8
5 km
Washington
46°
50 km

Figure 3. Photic behavior of Dendrobeania larvae during the two hours immediately following release from ovicells. Behavior is monitored in a glass tube illuminated from one end; numbers of larvae are counted in the dark and light half.

A- light half
B- dark half
open triangles (apex up) - replicate one
closed triangles (apex down) - replicate two


NUMBER OF LARVAE
0
2
4
6
8
10
12
10 20 30 40 50 60 70 80 90 100 110 120
TIME (MIN)

A


NUMBER OF LARVAE
0
2
4
6
8
10
10 20 30 40 50 60 70 80 90 100 110 120
TIME (MIN)

B

Figure 4. Numbers of larvae settled in shaded and unshaded halves of petri dishes over a 24 hour period. Larvae were added to petri dishes at least 8 hours before darkness.

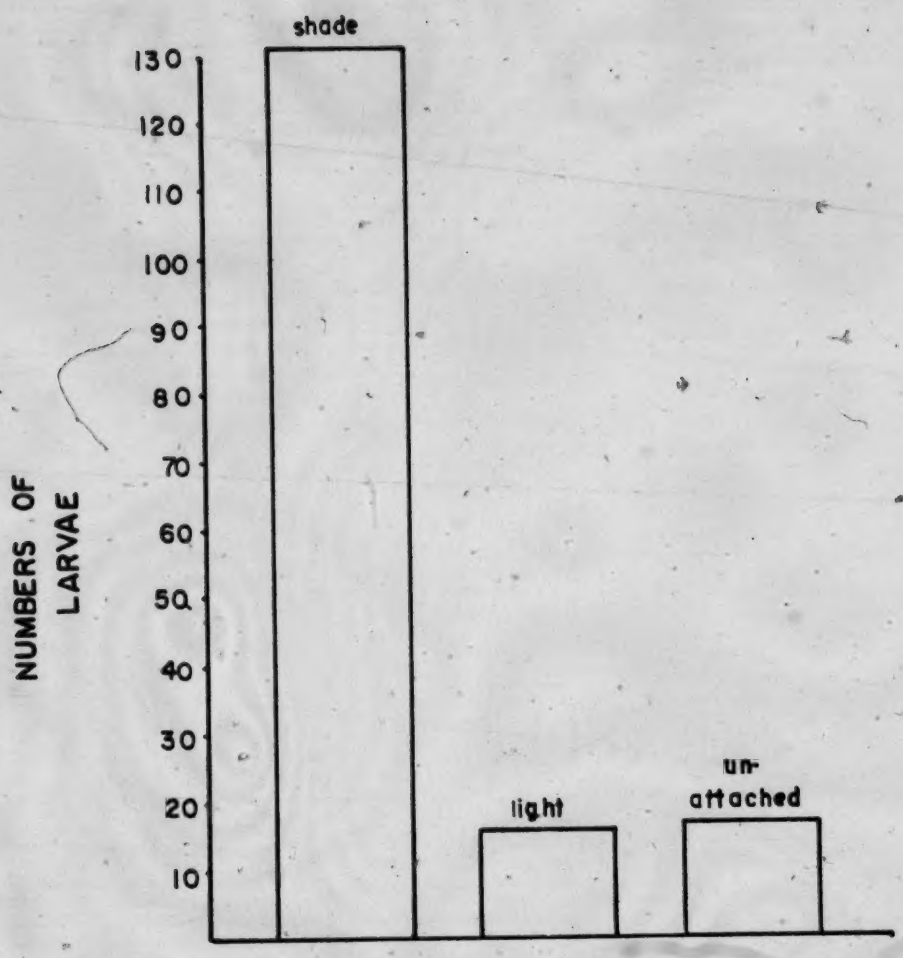
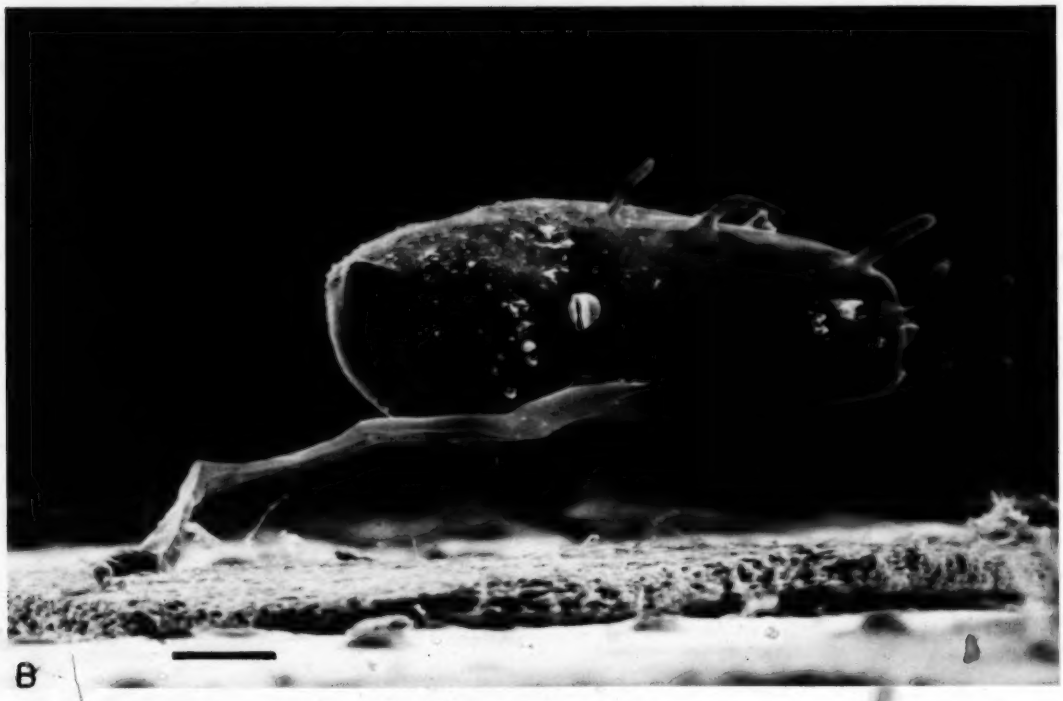

shade
130
120
110
100
90
80
70
60
50
40
30
20
10
NUMBERS OF LARVAE
light
un-attached

Figure 5. Comparison of the substrate relationship of Dendrobeania pre-ancestrulae and ancestrulae.

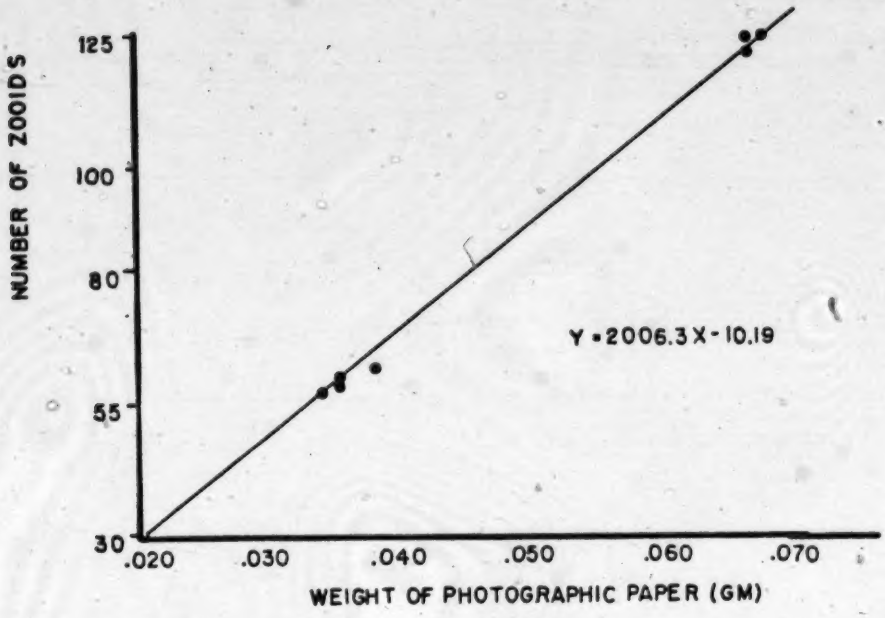
A- The pre-ancestrula remains encrusted on the substrate from the initiation of metamorphosis until approximate-four to five days post-settlement. The pre-ancestrula figured is one - two days post-settlement. Scale= 40 cm.

B- The pre-ancestrula at five to six days post-settlement is usually supported off the substrate by a rhizoid. Scale= 100 cm.



B

Figure 6. Calibration of number of zooids against weight of photographic paper and against underwater weight of colonies.


NUMBER OF ZOOIDS
125
100
80
55
30
.020
.030
.040
.050
.060
.070
Y = 2006.3X - 10.19
WEIGHT OF PHOTOGRAPHIC PAPER (GM)

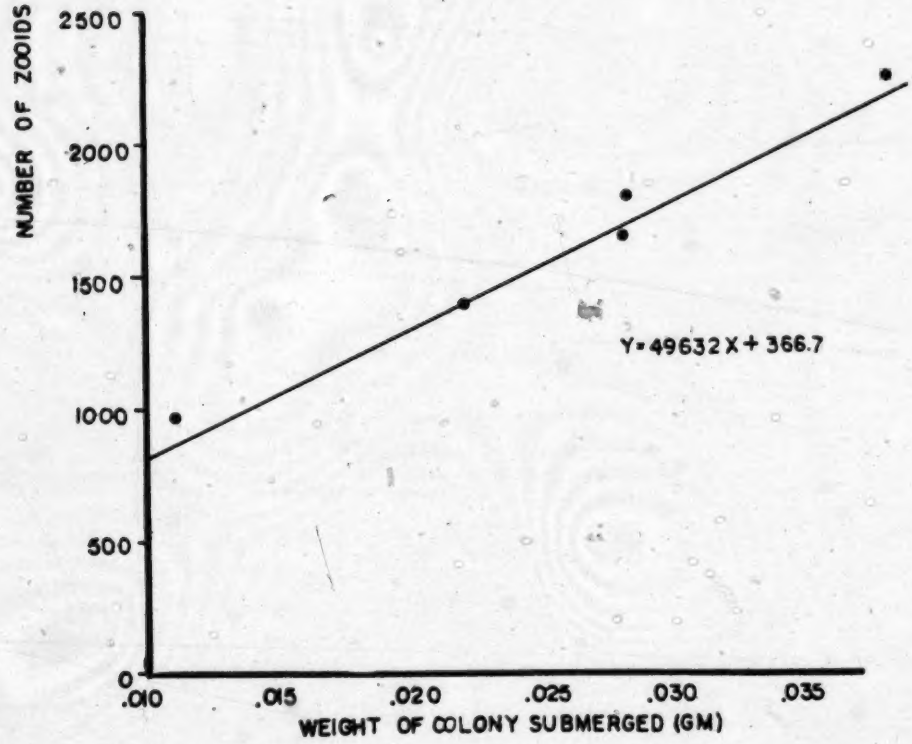

NUMBER OF ZOOIDS
2500
2000
1500
1000
500
0
.010
.015
.020
.025
.030
.035
Y = 49632X + 366.7
WEIGHT OF COLONY SUBMERGED (GM)

Figure 7. Calibration of Dendrobeania colony wet weight against colony dry weight.

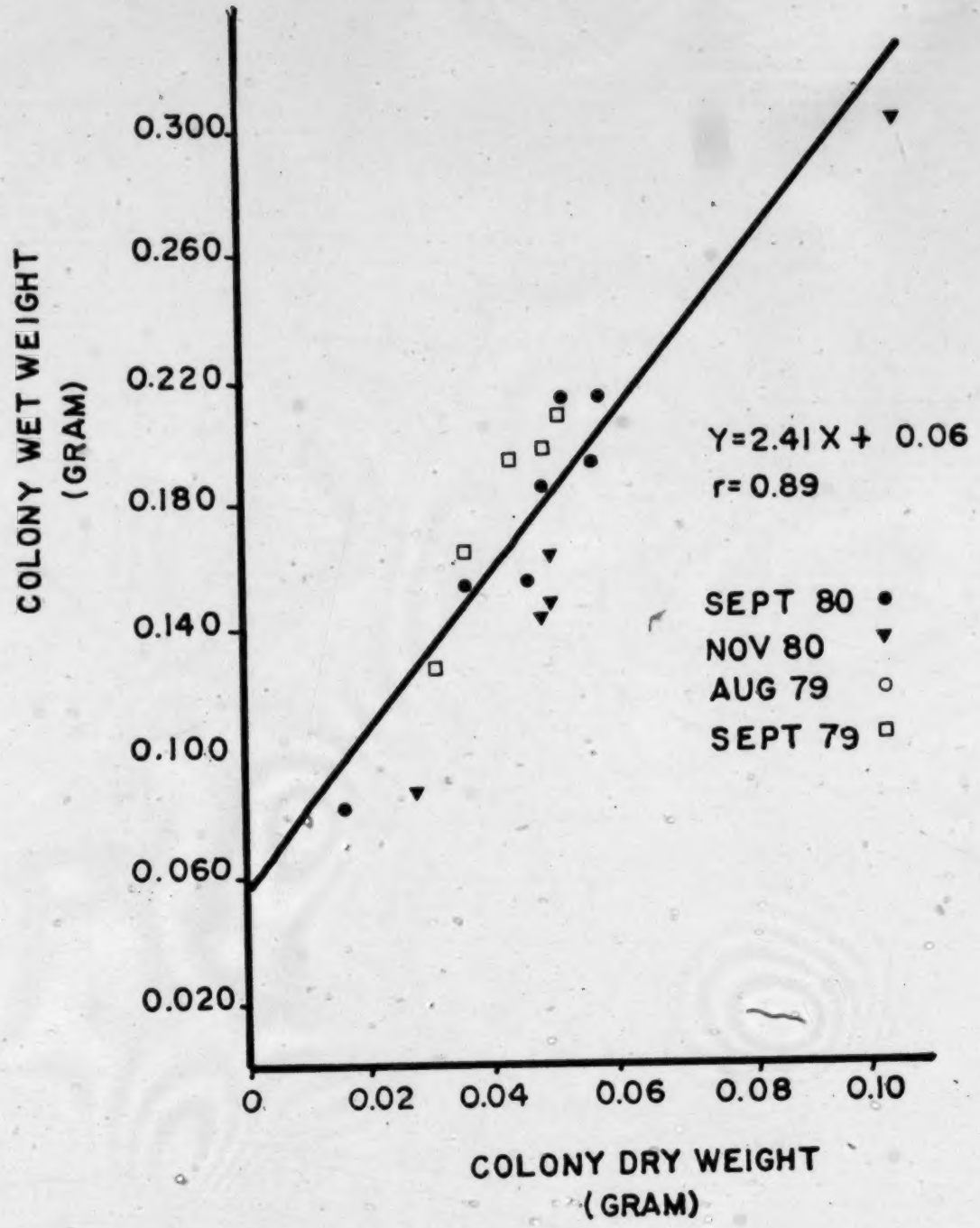

COLONY WET WEIGHT
(GRAM)
0.300
0.260
0.220
0.180
0.140
0.100
0.060
0.020
0
0.02
0.04
0.06
0.08
0.10
COLONY DRY WEIGHT
(GRAM)
Y=2.41X + 0.06
r=0.89
SEPT 80
NOV 80
AUG 79
SEPT 79

Figure 8. Astogeny (budding pattern) of Dendrobeania from two to five months post-settlement.

A- The initial bi-directional budding pattern at 2 months post-settlement. Each zooid is about 1 mm long.

A... ancestrula

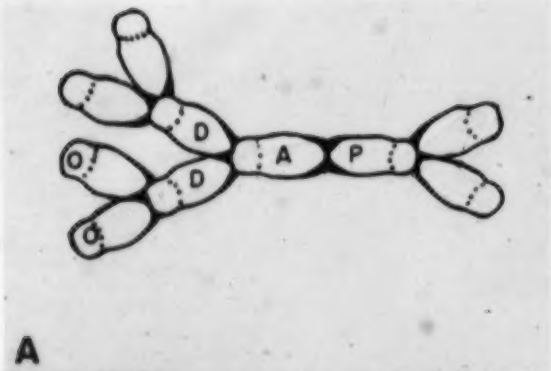
D... distal

P... proximal

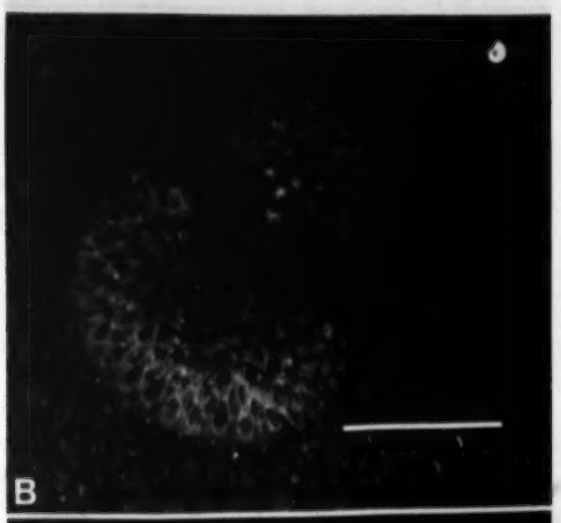
O... operculum

B- Colony form at 3 months post-settlement. Scale= 1 cm.

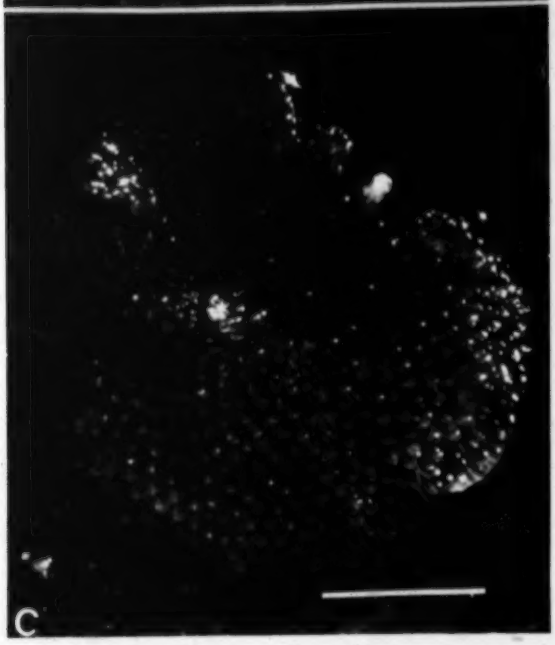
C- Colony form at 5 months post-settlement. Some colonies continue growing bi-directionally as in B. Scale= 1 cm.



A



B



C

Figure 9. Growth of Dendrobeania (mean number of zooids/month, n= 12 colonies) from January, 1980 to October, 1981.

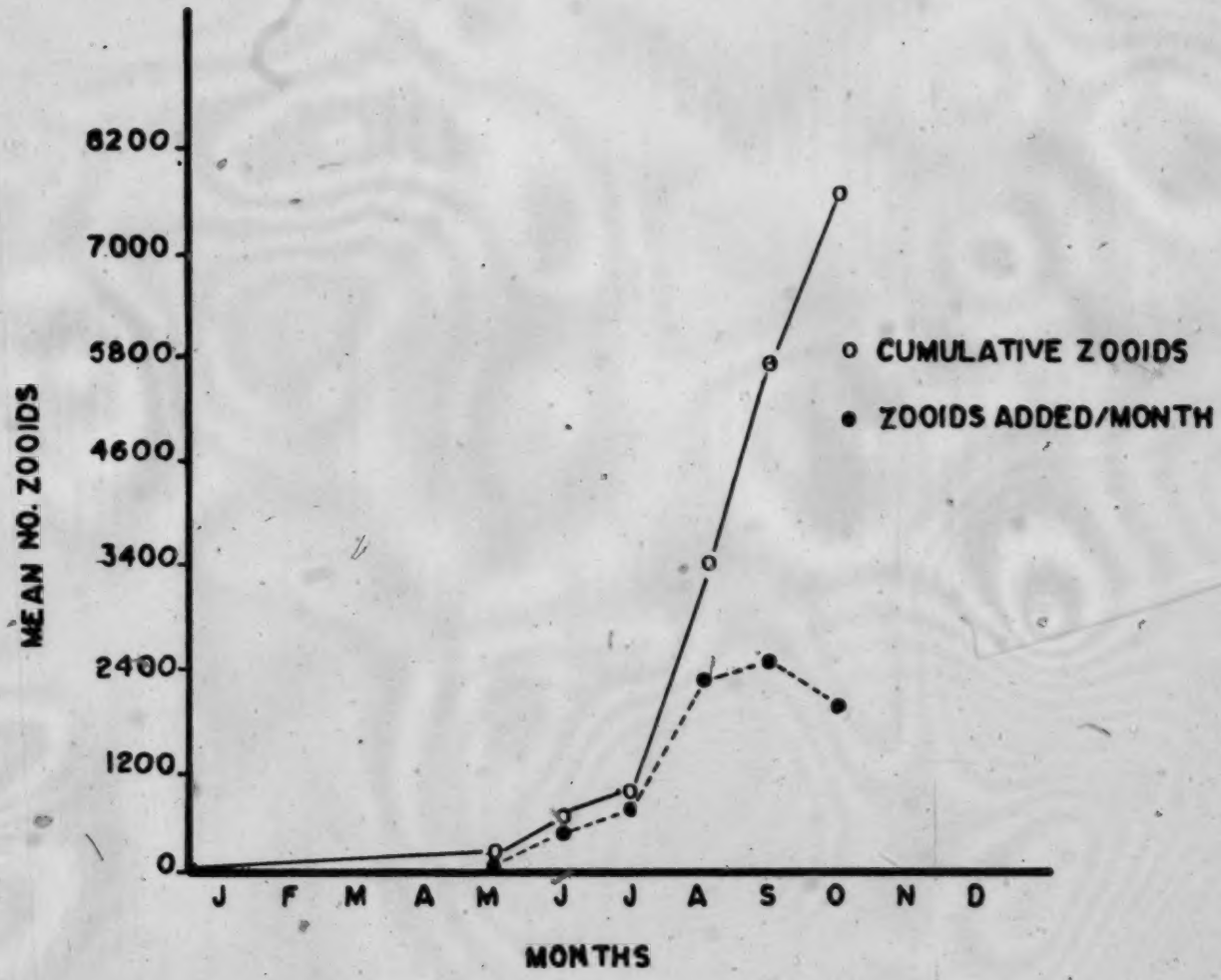

8200
7000
5800
4600
3400
2400
1200
0
MEAN NO. ZOOIDS
J F M A M J J A S O N D
MONTHS
o CUMULATIVE ZOOIDS
• ZOOIDS ADDED/MONTH

Figure 10. Monthly fecundity (mean number of embryos/gm, n= 5 colonies) of Dendrobeania colonies from August, 1979 to February, 1981.

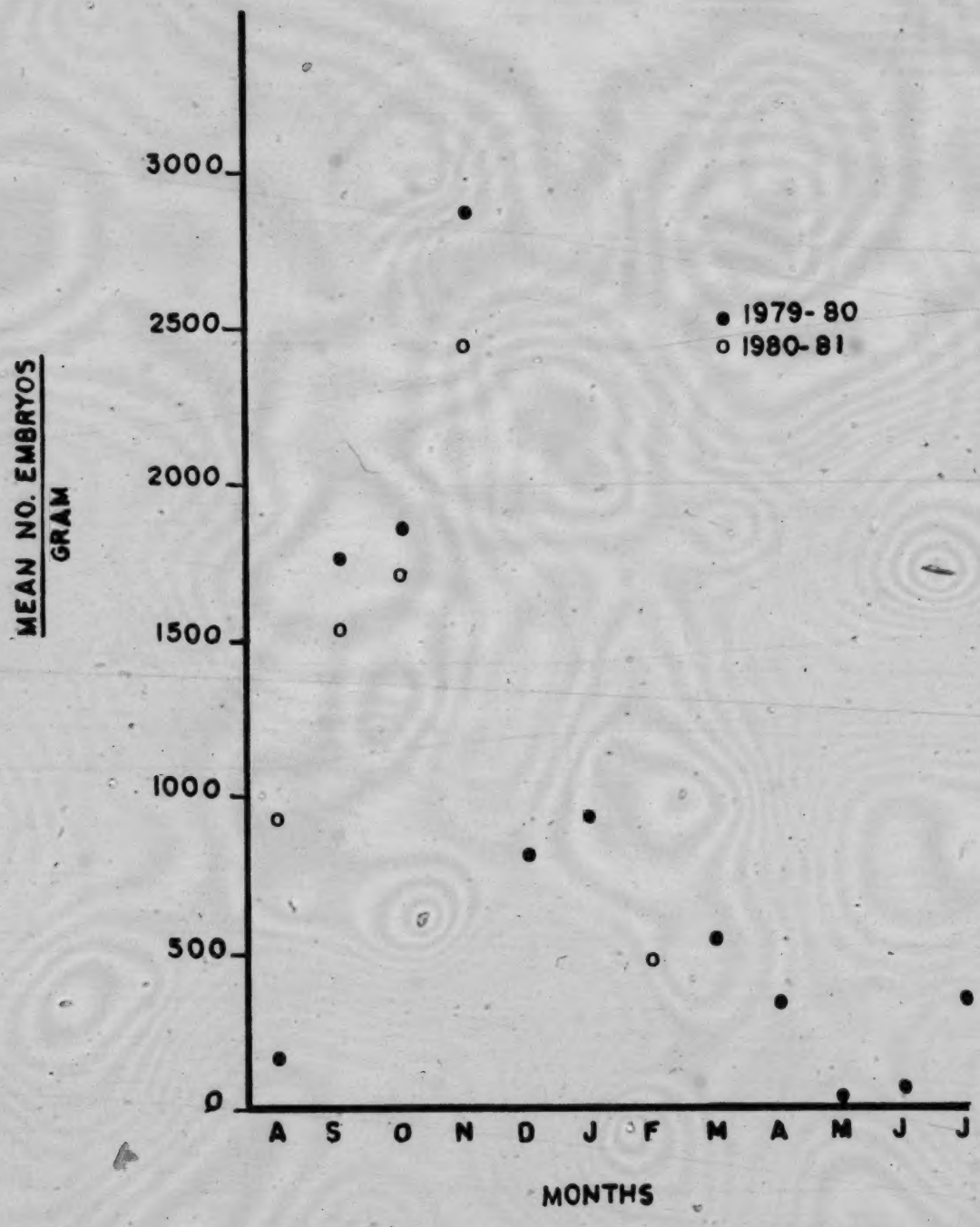

MEAN NO. EMBRYOS
GRAM
3000
2500
2000
1500
1000
500
0
● 1979-80
o 1980-81
A S O N D J F M A M J J
MONTHS

Figure 11. Seasonal surface temperature regime at Friday Harbor Laboratory (courtesy of David Duggins, Marine Technician, Friday Harbor Laboratory).

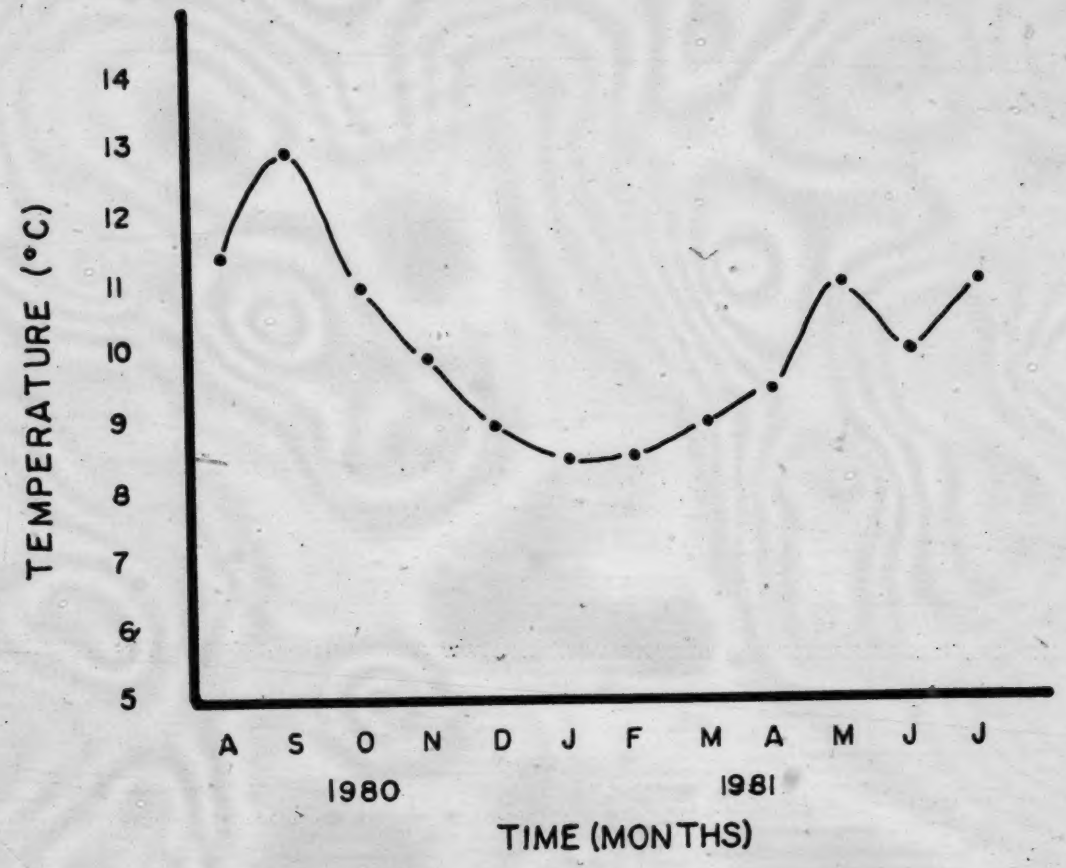
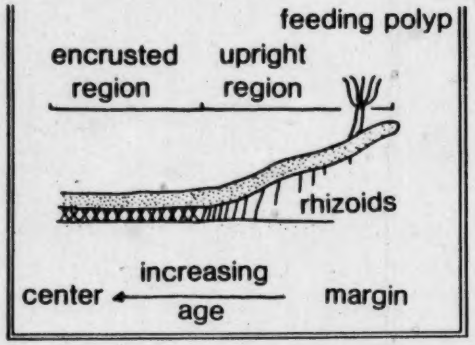
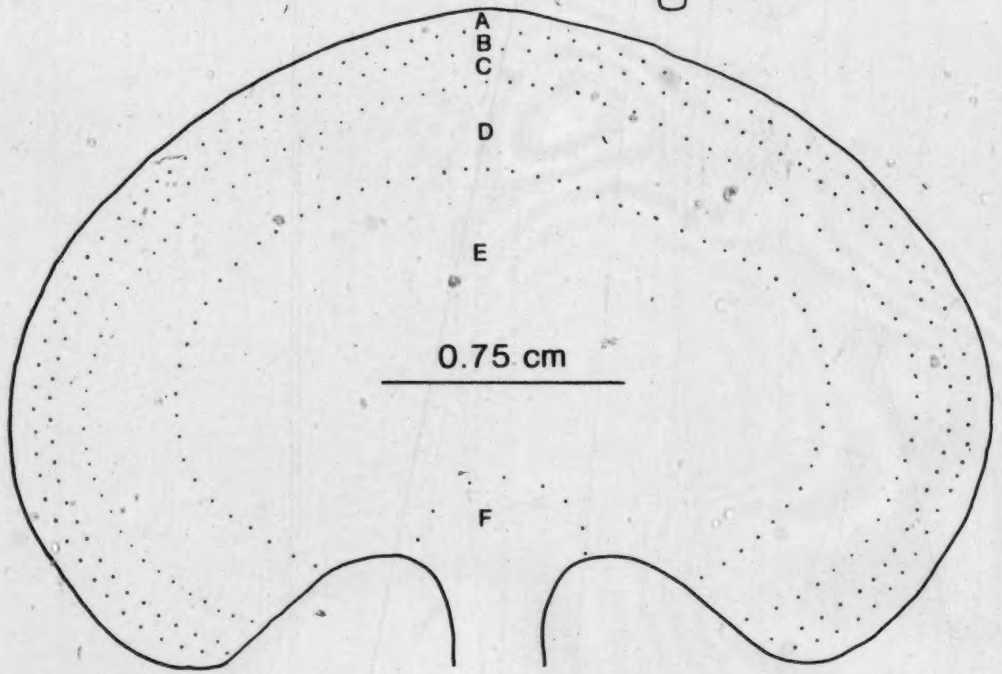

TEMPERATURE (°C)
14
13
12
11
10
9
8
7
6
5
A S O N D J F M A M J J
1980
1981
TIME (MONTHS)

Figure 12. Intra-colonial zonation of Dendrobeania. The inset is a cross-sectional view of one half of a colony, from the center to the growing margin, and displays the relationship of the attachment rhizoids to the substrate. Each measurement is taken as a line perpendicular to the margin and is a mean of 5 replicates/colony averaged over 22 colonies (see Table 5 for mean of five replicates/colony).

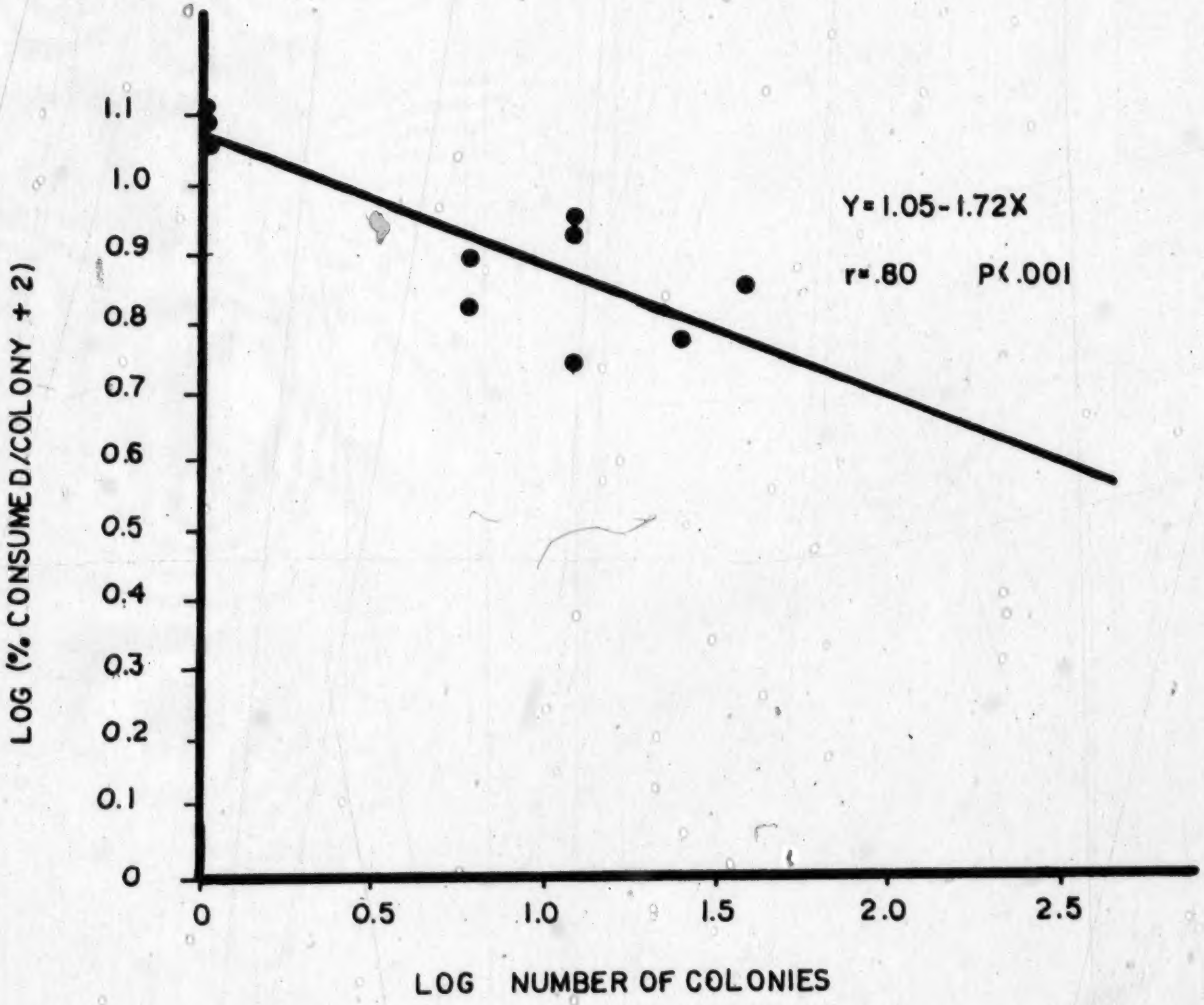


- brown body
- oocyte
- ovicell containing embryo
- rhizoid
- spines



DISTANCE FROM MARGIN TO BEGINNING OF INDICATED ZONE (CM)

Figure 13. Log - log plot of the relative percent of each colony consumed by Dirona albolineata and D. aurantia as a function of the number of colonies offered in each trial.


LOG (% CONSUMED/COLONY + 2)
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
0.5
1.0
1.5
2.0
2.5
LOG NUMBER OF COLONIES
Y=1.05-1.72X
r=.80 P<.001